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The restoration of plant pollinator interactions

The restoration of plant-pollinator interactions

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ABSTRACT

1. Restoration schemes are normally evaluated in terms of whether target species establish. While this is convenient information, it does not reveal how species interact in restored systems or how sustainable restored systems are.
2. This study first investigated old and restored hay meadows and then old and restored lowland heathlands. Sites were compared and contrasted with respect to plant-pollinator interactions. Both structural and functional aspects of the biodiversity were quantified. The latter was done through the application of quantitative food web statistics.
3. Fieldwork involved sampling flower-visiting insects, while laboratory work involved analysis of the pollen carried on insect surfaces. There was considerable variation in community structure among study sites of both habitats. Despite this variation, the meadows were functionally similar. For the heathlands, both flower visitation patterns and quantitative pollen transport patterns differed among study sites. This is concluded partly to be an artefact of the age of the restored heathlands that will disappear as they mature.
4. Heathland interaction webs were analysed for the presence of compartments. Although such compartments were concluded to be atypical for heathlands, the method for compartmentalization analysis may not have been suitable for detecting very small web compartments.
5. A study considered the impact of honeybees on bumblebees and found a negative association between these bees. However, no mechanism was confirmed to account for this.
6. Thrips pollination was investigated on the heathlands. Thrips were restored on all heathlands and found to affect a significant fraction of the seed set in three heathland plant species.
7. Restoration of plant-pollinator interactions was successful. Although structurally different communities had established on restored sites, study sites belonged to the same broad habitat categories and appeared to function in broadly the same ways.

For

my

Family

Jim said bees wouldn't sting idiots; but I didn't believe that, because I had tried them lots of times myself, and they wouldn't sting me.

Mark Twain, *Adventures of Huckleberry Finn*

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It is a luxury to be able to study something in detail for three years and discover how surprisingly little was known about that something. Ecology is a great jigsaw puzzle with so many of its pieces still missing. It has been a great privilege to be part of a 'search team' here in Bristol.

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AUTHOR'S DECLARATION

I declare that the work in this dissertation was carried out in accordance with the Regulations of the University of Bristol. The work is original except where indicated by special reference in the text and no part of the dissertation has been submitted for any other degree. Any views expressed in the dissertation are those of the author and in no way represent those of the University of Bristol. The dissertation has not been presented to any other university for examination either in the United Kingdom or overseas.

Mikael Lytzau Forup

Bristol, January 7th 2003

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CHAPTER ONE

Introduction

CHAPTER ONE

Introduction

1.1 Restoration ecology

Ecosystems are degraded when underlying ecological processes have been impaired, thereby causing change in the structure and functioning of the system (Naeem *et al.* 1994; 1995). The effects of this can include a reduction in conservation value, the loss of mutualistic associations, such as plant-pollinator relationships (Kevan and Baker 1983; Allen-Wardell *et al.* 1998), and shifts in inter-specific competition caused by an altered nutrient availability (Grime 1979; Aerts and Berendse 1988; Gerdol *et al.* 2000). The types of degradations that are considered in restoration ecology usually have anthropogenic causes. Therefore, restoration ecology can be viewed as the study of how to repair anthropogenic damage to the integrity of ecological systems (Cairns and Heckman 1996).

If left alone, degraded systems may eventually recover and the speed of this recovery is termed 'resilience' (Tilman and Downing 1994). When humans speed up the process of recovery, they perform an ecological restoration. Strictly speaking, however, it is only when a replicate of the original community has been reinstated with similar species composition, species interactions, age and size characteristics that 'restoration' has been achieved. If a scheme is only partially successful, the result is 'rehabilitation'. However, it can be difficult to determine if or when restoration has been achieved, because we rarely know the exact composition of the original ecosystem.

1.2 The 'fuzzy target' and 'moving target' problems

The problem of not knowing exactly what to restore an ecological community to has been termed the 'fuzzy target' problem (Simberloff 1990b). One way to fill this gap in knowledge is to study communities that are similar to the one we want to restore (Aronson *et al.* 1993; Pratt 1994; Aronson and le Floc'h 1996; White and Walker 1997). However, such extrapolations only offer an approximation as to what was present on a restoration plot prior to disturbance. The different location of the reference or control site might mean that a

different community has developed here due to differences in e.g. the soil substrate, the climate, the structure of the regional species pool, etc. Also, it is difficult to know if the reference community is not itself disturbed in some way. Consequently, unless the restoration site was thoroughly studied prior to its disturbance, we may only have a loose idea of what to restore.

Another complication is the fact that ecosystems change unpredictably in time due to fluctuating physical factors, such as the climate and soil nutrient levels, or due to biotic factors, such as species invasions and cyclic successions (Connell and Slatyer 1977; Simberloff 1990b; Hobbs and Norton 1996). For example, cyclical change has been documented for the Breckland heathlands where, under constant grazing pressure, the vegetation alternates between a *Calluna vulgaris* (L.) Hull-dominated state and a *Pteridium aquilinum* (L.) Kuhn-dominated state (Watt 1955). In a Breckland restoration scheme, which state of the cycle should be aimed for? This has been termed the 'moving target' problem (Simberloff 1990b).

In practise, restorationists often settle for less ambitious objectives in restoration schemes. Even so, due to the 'fuzzy target' and 'moving target' problems, they are still unable to evaluate the actual degree of restoration that has been achieved. For example, an objective can be to restore a 'wildflower meadow', with little or no regard paid to the original meadow community of the site, and using equally broad characteristics to determine the outcome of the scheme that usually focus on the reinstatement of desired plant species. For example, in a heathland restoration scheme, success can depend solely on the reinstatement of the dominant plant species, heather, *Calluna vulgaris* L. (Hull) (Anderson 1995). In contrast, associated species of plants, animals and microorganisms are often ignored, perhaps with reference to an assumption that they will find their own way onto the restored site. However, this approach poses some problems: even though a certain structure has been achieved, the sustainability of the system is at risk because vital processes and links may not have been understood and restored, nor have the degrading agents necessarily been arrested (Ehrenfeld and Toth 1997; Palmer 1997).

1.3 The 'field of dreams' hypothesis

The notion that it could be adequate to simply reinstate some basic community structure has been termed the 'field of dreams' hypothesis (Palmer 1997): if the restoration scheme has lead to the right habitat structure, species associated with the desired community will

eventually migrate onto the site by themselves. As far as I am aware, the vast majority of restoration schemes follow this approach to some extent, but whether it actually works remains untested. Certainly, the time scale will vary for different species, communities and localities (Bradshaw 1987; Pratt 1994). For example, in the 1930s a scheme was initiated at the University of Wisconsin that aimed at restoring tallgrass prairie on abandoned farmland. This is the oldest restoration scheme on record, yet fifty years later the community was still a depauperate version of the natural model, of which there are intact patches in the landscape (Jordan *et al.* 1987).

If the aim of an ecological restoration is to preserve a rare or threatened community, the field of dreams approach may not realistically restore the system, because source populations can be too rare or too far away to colonize the restoration plot. Species show huge differences in dispersal ability and many are increasingly faced with having to cross barriers. For example, the movement of woodland herbs between fragments of woodland set in a 'sea' of agricultural habitat may be almost impossible, because these herbs cannot establish 'stepping stone' populations in the extreme conditions of open land. In order to promote species migration in a highly fragmented landscape, restoration projects may therefore seek to provide corridors between islands of natural or semi-natural habitat (e.g. Bennet *et al.* 1994; van Dorp *et al.* 1997). However, in many cases this is unlikely to happen under the socio-economic constraints of ecological restorations, wherefore the restorationist may have to introduce certain species himself (Bradshaw 1987; Pratt 1994). Moreover, such corridors may not provide suitable conditions for all species or their mutualist partners, e.g. because of edge effects (Murcia 1995; Donohue *et al.* 2000). For example, ant-dispersed herbs (like those described by Handel *et al.* 1981) may not be found in corridors if the conditions are not suitable for ants.

Assembly rules are a further complication. These rules govern the different community endpoints that can arise depending on the invasion sequences of species from the same species pool (Drake 1990; Murcia 1995). Where restorationists have specific community endpoints in mind, the restoration project should therefore take into account the sequence in which species are introduced (Luh and Pimm 1993). However, these rules are poorly understood and, consequently, ignored in many restoration projects.

Finally, local ecotypes may no longer exist and although propagules of a given species can be introduced from elsewhere, or the species eventually colonize the site by its own accord, the restoration will never be strictly complete (Montalvo *et al.* 1997).

1.4 When are ecological restorations carried out?

Restoration schemes are carried out for a number of reasons, ranging from purely aesthetic ones, such as building desirable landscape characteristics, over concerns related to biodiversity, e.g. the conservation of rare species and habitats, to purely functional reasons, such as the restoration of an ecosystem service like water purification. Here I will focus on biodiversity.

In the United Kingdom, conservation of rare species and habitats is legally binding under the European Union's Habitat Directive[1] while the sustainable use of biodiversity is pledged under the Convention on Biological Diversity[2]. However, many of our species and habitats are still declining, e.g. species of bumblebee (Williams 1982; Benton 2000), birds (Chamberlain *et al.* 2000; Robinson and Sutherland 2002), plants (Rich *et al.* 1998; Donohue *et al.* 2000) and, at the habitat level, heathlands (Blackstock *et al.* 1995; Rose *et al.* 2000) and grasslands (Blackstock *et al.* 1999; Hulme *et al.* 2002). Even if a species has been afforded some protection by nature reserves, the decline can continue if populations are small and fragmented and the reserves are small and suffer from edge effects (Murcia 1995; Bell *et al.* 1997; Meiners *et al.* 2000).

'Ecosystem function' refers to the physical and chemical processes that are governed by biological activity in a given ecosystem (Naeem *et al.* 1995). When ecosystems lose biodiversity, they may show impaired ecosystem function (Naeem *et al.* 1994; Tilman and Downing 1994; Naeem *et al.* 1995; Tilman *et al.* 1996; Tilman 1999). However, the role of biodiversity for ecosystem function is complex, partly because species vary in importance. For example, a keystone species is one that performs a community role, which is disproportionately large for the density or biomass of the species (Paine 1969; Simberloff 1990a; Berlow 1999). To illustrate this, species of ant are the chief seed dispersers of some of the fynbos plants of South Africa (Bond 1994; Christian 2001). In the absence of these ants, seed predation is high and the overall result is poor plant recruitment. Hence the ants are keystone species because they maintain plant community structure. However, most individual species are unlikely to be this important for the functioning of the entire system, but they can be part of functional groups that are. For example, the majority of pollination systems are generalised, at least in the north-temperate zone (Waser *et al.* 1996; Johnson and Steiner 2000) and while individual pollinator species may not quantitatively be very

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[1] Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora, European Union 1992.
[2] Rio World Summit, United Nations 1993.

important for plant pollination, a pollinator community has to be in place for pollination to take place at all. Furthermore, there could be a degree of redundancy in these biodiversity-driven processes (Lawton 1994), whereby numerous, rare species maintain a back-up of function under extreme events. Consider a hypothetical example in which a common species of bumblebee has suddenly experienced a severe outbreak of parasites that has caused populations to crash. Although the pollination effected by this species has declined markedly, other species are unaffected by the parasite, feed on flowers and effect adequate pollination, perhaps even in higher numbers because they are experiencing competitive release. It is partly the potential for functional redundancy among the pool of colonists on restored sites that led to the formulation of the field of dreams hypothesis: because of this redundancy, it may be possible to set a minimum for restoration that ensures proper functioning (Palmer 1997).

1.5 Problems in current restoration ecology

Restoration ecology suffers both from the lack of a general template to work from and from inadequate communication among practitioners and theorists. Often restoration schemes are carried out on an *ad hoc* site- and situation-specific basis, with little regard for experimental design and the general advancement of the science (Hobbs and Norton 1996; Montalvo *et al.* 1997). Hobbs and Norton (1996) advocated the need for a general template. In their view, restoration projects should consider the following key points: 1) identify the processes leading to degradation or decline; 2) develop methods to reverse or ameliorate the degradation or decline; 3) determine realistic goals for re-establishing species and functional ecosystems, recognising both the ecological limitations on restoration and the socio-economic and cultural barriers to its implementation; 4) develop easily observable measures of success; 5) develop practical techniques for implementing these restoration goals at a scale commensurate with the problem; 6) document and communicate these techniques for broader inclusion in land-use planning and management strategies; and 7) monitor key system variables, assess progress of restoration relative to the agreed-upon goals, and adjust procedures if necessary.

Since restoration projects sometimes occur with little or no consideration to these key processes, some projects risk failing, because the degrading agents have not been addressed and continue to operate. However, even where the degrading influences have been addressed successfully, the restoration may still fail for a number of reasons. Most

important among these is the failure to consider the sustainability of the restored system, e.g. where crucial, but possibly inconspicuous, reproductive mutualisms have not been reinstated (Kevan 1991).

1.6 Reproductive mutualisms

Successful reproduction is essential for the long-term persistence of a population in any community. Plants have adopted different strategies in this respect, ranging from vegetative reproduction, through agamospermy to anemophily and entomophily (Grime 1979; Culley *et al.* 2002). It is the latter, entomophily or insect-mediated pollination, which is the focus of the work presented in this thesis.

Reproductive mutualisms occur when animals feed on plant floral rewards and, in so doing, cause fertilization by depositing pollen onto flower stigmas. Pollination is important for the sustainability of plant communities, both in terms of the quantitative seed production, but also for genetic reasons. Because insects primarily visit flowers with the purpose of feeding on floral resources, they can be very efficient at effecting cross-pollination and thereby reduce inbreeding (Spira 2001).

Plant-pollinator interactions are normally generalised (Woodell 1979; Kevan and Baker 1983; Waser *et al.* 1996; Johnson and Steiner 2000). Although the evolutionary mechanisms of this are difficult to decipher (Ollerton 1996), it makes sense ecologically. Reproductive success is more likely for plants with diverse pollinator associations, because this to some extent cancels out the variations in the relative abundance of species (Spira 2001). Likewise, selection favours pollinators with broad plant bases, because this reduces the negative effects of fluctuating abundances in individual plant populations among years. Moreover, plant and pollinator species also vary in their relative importance as food sources and pollinating agents, respectively (Schemske and Horvitz 1984). A study by Memmott (1999) suggested that wild carrot, *Daucus carota* L., could be a keystone species in an English meadow community. Here a wide range of insect species came to feed mainly on the pollen of the carrot flowers and no other plant species was visited as often as wild carrot. Thus, because the species was important for feeding the pollinator community, this could have positive effects on other plant species, since generalist visitors to *D. carota* also visit and pollinate other plant species. Similarly, just as plants differ in quality from an insect point of view, the insect visitors also vary in quality from a plant point of view. For

example honeybees, *Apis mellifera* L., can be locally abundant but are considered inferior pollinators to the less abundant bumblebees, *Bombus* spp. Latr. (Westerkamp 1991).

Ecological restorations rarely consider pollination. When they do, the focus is normally on the conservation of rare plants species (e.g. Walker and Powell 1999; Wilcock and Jennings 1999), or rare insects, which also 'happen' to be pollinators (e.g. Thomas and Harrison 1992; Thomas *et al.* 1998; Schultz 2001) rather than on pollination as an ecosystem process (but see Handel 1997 for an exception).

1.7 Food webs and pollination biology

The majority of the plant-pollinator interactions described in the literature only consider the interactions between a few species in a community (Waser *et al.* 1996). More often than not, the focus is placed unilaterally on the plant species in these mutualisms (Bronstein 1994). For example, studies can consider the insect visitors to a given plant species at a given geographical location (e.g. Mahy *et al.* 1998; Navarro 2000). However, at other times, only subsets of the insect visitors are considered, such as specific orders like Hymenoptera and Lepidoptera, etc. (Waser *et al.* 1996). Although plant ecology is often assumed have a longer tradition than ecological entomology, early work actually considered insects as flower visitors (e.g. Müller 1881; Knuth 1906; 1908; 1909). Nonetheless, workers are sometimes, perhaps unconsciously, biased towards neat concepts, such as the classical pollination syndromes. Insects which do not easily 'fit' into these syndromes, risk being considered atypical and ignored, or insects may generally be thought too variable in both space and time to warrant study (Waser *et al.* 1996). Despite recent advances in the field (e.g. Reed 1995; Memmott 1999; Dicks *et al.* 2002), community-wide studies of plant-pollinator systems are still relatively rare and often poorly understood (Corbet 1991; Bronstein 1994; but see Ollerton and Cranmer 2002). Yet such studies can help us overcome some of the conscious and unconscious biases, which prevent us from identifying true pollination systems.

One way of analysing quantitative visitation and pollen transport data is through the application of food web theory. Food webs show the flows of energy and materials among organisms that result when some organisms eat or consume other living organisms or their parts (Pimm 1982; Cohen *et al.* 1993). The original purpose of food webs was to show the impact of predation and competition (e.g. Smith and Slobodkin 1960; Paine 1966; Menge and Sutherland 1976; Havens 1993). However, food webs can also be applied to other types

of interactions, such as successional facilitation (Hacker and Gaines 1997; Olff *et al.* 1999) and mutualisms (e.g. Fonseca and Ganade 1996; Memmott 1999; Dicks *et al.* 2002). The standard food web statistics are connectance and linkage density. Connectance is the fraction of realized trophic interactions over the total number of possible interactions (Martinez 1991) and is a convenient way of comparing webs in terms of their complexity, while linkage density is the number of links per species (Pimm *et al.* 1991). They are both important statistics for community dynamics and relate directly to community function. Consequently, they are also of clear relevance to restoration ecology (Cohen *et al.* 1993).

Comparing interaction webs between pristine and restored habitats may therefore be a way of solving some of the problems in restoration ecology. Although they do not solve the 'fuzzy target' and 'moving target' problems, the quantification of key linkages in the processes on reference systems provide useful targets to aim for in the restoration process. Although there may be structural differences in the biodiversity of reference systems, i.e. differences in the species composition of the communities, the key processes are likely to be similar. Therefore webs can be used both for the planning and evaluation stages of ecological restorations.

1.8 The aim of this study

The aim of the work presented in this thesis is to determine whether restoration schemes reinstate the interactions between plants and pollinators. A food web approach is used that will both provide data on the structural and functional aspects of the biodiversity on the study sites. Structural aspects of biodiversity concern the presence and abundance of species, while functional aspects concern the interactions between biodiversity and ecological processes. Moreover, the work will also provide much needed data on plant-pollinator interactions at the community level.

1.9 Meadows and heathlands

Both hay meadows and lowland heaths were used in the study. The former was used in the pilot work, which led on to the main study on the latter habitat. Hay meadows and heathland are comparable is some aspects, for example, both are nutrient-poor systems that are maintained through anthropological activities. However, while hay meadows are rich in plant species, heathlands have few plant species. Both can be rich in pollinators.

1.10 Thesis organisation

The pilot study on hay meadows is described in Chapter 2. Here I examine the plant-pollinator interactions on two pairs of old and restored meadows in the Bristol area, asking whether similar plant-pollinator relationships are found on these meadows.

In Chapter 3, focus is on dry lowland heath in Dorset. Here the sampling design employed in Chapter 2 is improved and four pairs of old and restored heathlands are studied. Are structural aspects of plant-pollinator relationships restored on the young heathlands and does this compare to the functional aspects of their biodiversity?

Chapter 4 investigates the potential presence of compartments in these webs, i.e. groups of plants and pollinators that interact more with each other than with other species that could therefore be useful units for pollinator conservation. Is there evidence of such compartments in the flower visitation and pollen transport data? Are they replicated in space and do visitation compartments translate into pollen transport compartments?

In Chapter 5 I investigate the potential impact of honeybees, *Apis mellifera*, on bumblebees, *Bombus* spp., on lowland heaths. Is there evidence of a negative impact?

Chapter 6 concerns a group of pollinators that is often ignored in pollination studies, namely thrips (Order: Thysanoptera). How abundant are they on old and restored heathlands and how important are they for the pollination on lowland heaths?

I conclude in Chapter 7 by bringing together the main findings of this thesis. What has been learnt about the restoration of plant-pollinator interactions and has a food web approach been useful in the evaluation of restoration schemes?

CHAPTER TWO

The restoration of plant-pollinator interactions on hay meadows

CHAPTER TWO

The restoration of plant-pollinator interactions on hay meadows

SUMMARY

Whether restoration programs successfully reinstate ecological interactions remains a contentious and largely untested issue. Here I investigate the restoration of interactions between plants and pollinators in English hay meadows. Insect visitation and pollen movement were quantified, at the community level, in two ancient and two restored meadows. For all meadows, Diptera and Hymenoptera, both in terms of species richness and abundance, dominated the flower visitors. Coleoptera, Lepidoptera and Hemiptera made up the remainder of the flower visitors. There was no significant difference between the restored and ancient sites in plant or insect species richness, plant or insect abundance, or the proportion of plant species visited. Plant species visited by insects were generalized with all having more than a single species of insect visitor. A slightly higher proportion of potential links between plants and insects was realized for ancient meadows leading to higher connectance values in their visitation webs. I also sampled approximately 400,000 pollen grains from the flower-visiting insects. There were no differences between ancient and restored sites in the amount of pollen being transported or the average number of pollen grains per insect. At both types of meadow, Hymenoptera carried most pollen, followed by Diptera. Again, generalization was the norm with all plants having more than a single species of pollen carrier. No difference was observed in the connectance of pollen transport webs between ancient and restored sites. Overall, there were few differences in the parameters I used to assess pollination, suggesting that pollination interactions have been successfully restored.

2.1 INTRODUCTION

2.11 Restoration of interactions

In most terrestrial restorations, emphasis is placed on reinstating easily measurable characteristics, such as the species composition of the vegetation. However, apart from restoring structural biodiversity, restoration schemes should also reinstate key linkages between species (Ehrenfeld and Toth 1997; Palmer 1997). It is the restoration of ecological processes, such as trophic interactions, decomposition rates, pollination and disturbance regimes, which may ultimately determine the success of a restoration (Hobbs and Norton 1996; Ehrenfeld and Toth 1997; Montalvo *et al.* 1997). For example, the apparently successful reinstatement of a plant community is unlikely to be sustainable if the plants are not pollinated. The aim of the work presented here is to quantify the linkages between flowering plants and pollinators in two ancient meadows and two restored meadows and thereby to assess the efficacy of the restoration programmes.

2.12 Interaction webs

The majority of interactions between individual plant and pollinator species are embedded in a complex web of such interactions (Waser *et al.* 1996). These plant-pollinator webs can be studied in the manner of conventional food webs (Jordano 1987; Petanidou and Ellis 1996; Waser *et al.* 1996; Elberling and Olesen 1999; Memmott 1999; Dicks *et al.* 2002). Memmott (1999) and Dicks *et al.* (2002) presented quantitative visitation webs for meadow communities, where the absolute abundance of each insect species and each flowering plant species was shown, along with the frequencies of interactions between them. Visitation webs can be used to study the restoration of pollination processes. Web statistics such as species number, species abundance, connectance and linkage density can all be readily calculated from visitation webs. These values, from reference sites and restored sites, can then be compared allowing the restoration project to be described in quantitative, rather than qualitative terms.

Moreover, if these statistics are measured for a number of sites, some measure of their natural variability can be assessed. Natural, physical and biological variability is a part of community structure (Kitching 1987; Warren 1989; Tavares-Cromar and Williams 1996) and one of the challenges facing restorationists is to develop tools for assessing acceptable

levels of variability among restored populations (White and Walker 1997). For example, we know that in food webs where large and small organisms eat each other, connectance should vary between 0.02 and 0.1 (Martinez *et al.* 1999). If, for example, a restored site ends up with a connectance value of an order of magnitude from these values, then the restorationist should be suspicious of the success of the project. There is considerable debate over how to assess restoration; including what constitutes a reference or comparison site and what metrics are most appropriate (Michener 1997; White and Walker 1997). Here I propose that looking at the interactions between species could prove a highly useful metric to quantify when comparing reference and restored sites.

2.13 Plant-pollinator webs

A quantitative visitation web shows the abundance of both flowers and insects, and the frequency with which each insect species visits each plant species. Therefore, such a web can be useful when comparing old and restored sites, because it provides an insect perspective on the quantity, quality and regularity in nectar and pollen supplies at each site. Conversely, if pollen is sampled from the flower visitors, data can also be gathered about which insects are the likely pollinators at the site and so provide a plant perspective on restoration success. Information on which insect species transport which pollen species can be used to construct pollen transport webs, allowing us to investigate whether the quantity and quality of pollen transporters at the restored site is equivalent to that at the reference site. Interestingly, the possibility exists that an entirely different assemblage of plant-visiting insects could be present at restored sites, but if pollen is transported in a similar manner then the restoration scheme could be successful from the perspective of the plant community.

2.14 Aims

Hay meadows represent some of the most species-rich plant communities in Britain, yet most have been lost to agricultural intensification (Rodwell 1992; Blackstock *et al.* 1999). Approximately 97% of British meadows have disappeared and many remain threatened (Feltwell 1992). Meadow restoration, along with meadow creation, is an important part of the conservation effort. Here I quantify the pattern of insect visitation and pollen movement in two ancient and two restored English hay meadows. My intention is to use visitation and pollen transport webs to characterize the plant-pollinator communities at these sites and

then to compare and contrast these webs. The specific objectives are threefold: (1) to determine whether the pattern of insect visitation is comparable in old and restored meadows; (2) to determine whether the pattern of pollen movement is comparable in old and restored meadows; and (3) to use the data to decide whether pollination has been successfully reinstated.

2.2 METHODS

2.21 Study sites

Four meadows classified as MG1 under the British National Vegetation Classification (Rodwell 1992) were chosen near Bristol in the south west of England (Table 2.1). The MG1 meadow is a typical lowland community, typified by an annual hay cut and the absence of livestock grazing. Meadow 1 and Meadow 2 were old meadows dating back to before agricultural intensification. They were therefore reference sites. In contrast, Meadow 3 and Meadow 4 were recently restored meadows. Meadow 3 was restored in the early 1990s. Prior to restoration, this meadow was degraded through frequent mowing (it was part of a golf course) and it is likely that fertilizer application took place to improve the sward. The restoration of this meadow simply involved the return to traditional MG1 management, i.e. an annual hay cut. Meadow 4 was established in 1981 in a section of a formal city park. The park, which originally consisted of steep slopes grazed by sheep, was landscaped in the 1920s and 1930s. In the time between landscaping and restoration, meadow 4 was a frequently mowed lawn where soil fertility was kept high by fertilizer application. The restoration of Meadow 4 consisted of the translocation of turfs from another meadow to a section of Meadow 4, some planting of wild flower plugs, some sowing of flower seed and a return to an annual hay cut (Helen Hall, Avon Wildlife Trust, *pers. comm.*). The restoration was proposed in 1980 and since then the site has been transformed to demonstrate how wildlife can be attracted into the heart of a city (Anon. 1989).

2.22 Flower visitation webs

A 100 m by 100 m plot was established in each of Meadows 1, 2 and 3, respectively. Within each plot, two 50 m transects were chosen at random on each sampling occasion. All of Meadow 4 was used, because of the small size of this meadow. Sampling began in early May when the plants were beginning to flower and was carried out every 13-15 days until the end of July 2000 when three of the meadows were cut. The hay was cut in Meadow 2 at the end of June and therefore only four samples were taken from this meadow compared with the six from the other three meadows. Sampling was carried out on dry, sunny days with moderate wind only.

In each transect, the identity of all flowering, non-grass plant species was recorded, along with the number of flower heads. Following plant identification, the transect was left for a minimum of five minutes to allow insects to re-disperse into the area. After this time the transect was walked again, this time capturing all the insects observed visiting flowers. A swathe of vegetation 2 m wide was sampled for flower visiting insects, with insects up to 1 m ahead being recorded. I made no *a priori* decisions concerning whether an insect was likely to be a pollinator; rather all insects visiting flowers were collected. All insects found on flowers were collected. They were either caught using a net or captured directly into a killing tube (2.5 x 8.5 cm) lined with a small paper bag. This paper bag and a paper disk, which lined the vial cap and was replaced after each catch, prevented insects from touching the sides of the glass vial, which could then be used for subsequent catches with a low risk of pollen contamination. Once an insect was anaesthetized, the bag containing the insect was removed from the glass vial; the bag folded shut and transferred to a larger killing jar. I identified hoverflies, butterflies and moths to species, all other insects were identified by taxonomists at the National Museum of Wales.

2.23 Pollen transport webs

A pollen reference collection was made from the flowers of the non-grass plant species found in or near the meadows during sampling. Flower buds were collected in the field and left to mature and open in the laboratory. Once the flower opened and the anthers dehisced, pollen was collected, stained with fuchsin pink and mounted on a microscope slide (Fægri and Iversen 1975). In the laboratory, each sampled insect was systematically dabbed with a 5 mm x 5 mm square of fuchsin pink gel (Kearns and Inouye 1993). Pollen storage areas were avoided, for example pollen baskets on bumble bees, as these contain pollen unlikely to be available for pollination. The forceps used for holding the square of staining gel were sterilized over a flame between insects.

Using the pollen reference collection, I identified the pollen on each insect collected from the meadows. Certain pollen grains were not easily distinguished under the light microscope. Hence the composites *Crepis biennis* L., *Crepis capillaris* L., *Crepis vesicaria* L. and *Hypochaeris radicata* L. were amalgamated into one species group while the buttercups *Ranunculus acris* L., *Ranunculus bulbosus* L. and *Ranunculus repens* L. were amalgamated into another. Pollen not matching any grains in the reference collection was recorded as 'unknown'. Only pollen grains recorded five or more times from an insect were

used in the analysis. This reduced the risk of pollen contamination, potentially occurring in the insect net or subsequent handling of the insect, biasing the results.

2.24 Flower groups

Since communities can consist of guilds of functionally similar species, the direct comparison of two or more interaction webs can show considerable taxonomic divergence, when functionally these webs may be very similar. In the literature, early attempts were made to classify plants with regard to the types of insect that visit their flowers (e.g. Delpino 1868, 1869; 1870, 1875; Müller 1881; Knuth 1906; 1908; 1909). This eventually resulted in the familiar pollination syndromes, which directly link the morphology of flowers to that of visiting insects. However, these approaches often fail to accommodate all entomophilous species in a given community, because they focus on clear-cut situations, such as specialised plant-pollinator mutualisms, which are not common. By modifying the existing classifications, especially that of Müller (1881) and Knuth (1906; 1908; 1909), it was possible to create a classification of the flower groups found on the MG1 meadow plants based solely on the flower characteristics of accessibility to floral rewards and flower density. Therefore, the classification reflects the niche types in the flower community. This classification is shown in Table 2.2.

2.25 Data analysis

The quantitative interaction webs were drawn by Dr Jane Memmott with a programme written in Mathematica™. In order to compare visitation in the restored and ancient meadows, the following statistics were calculated for each visitation web: 1) the number of flowering plant species, insect species and flower groups; 2) flower and insect abundance; 3) proportion of plant species visited; 4) the median number and range of insect species visiting each plant species; 5) the median number and range of plant species visited by each insect species; 6) linkage density based on both plant species and flower groups; 7) web connectance based on both plant species and flower groups; and 8) the Berger-Parker dominance index for the number of plants visited by each insect species.

In order to compare pollen movement in the old and restored meadows, the following statistics were calculated for each pollen transport web: 1) the number of pollen species groups; 2) pollen abundance; 3) the proportion of pollen groups being carried at each site; 4) mean pollen abundance per insect species; 5) the median number and range of pollen

species found on each insect species; 6) the median number and range of pollen transporters per plant species; 7) linkage density based on both plant species and flower groups; 8) web connectance based on both plant species and flower groups; and 9) the Berger-Parker dominance index for the number of pollen groups carried by each insect species.

The ratio of links per species is called linkage density, *L*, and has the formula:

$$L = \frac{l}{I + P} \qquad \textbf{Equation 2.1}$$

where *l* is the number of observed linkages and *I* is the number of insect species in the sample and *P* is the number of plant species. Connectance, *C*, is simply a measure of web complexity and is the fraction of realized links in the web. In these plan-pollinator webs it has the formula:

$$C = \frac{l}{IP} \qquad \textbf{Equation 2.2}$$

The links (*l*) in any calculation of connectance are counted simply as present or absent and no measure of link frequency is involved. Consequently, this statistic could hide a difference in visitation pattern, since an insect could specialize in a particular plant, and occasionally visit others, or it could divide its visits equally between species. To overcome this problem, I calculated a plant dominance index for each insect species, quantifying the equitability of both their flower choices and the equitability of the pollen species they transported. I used the Berger-Parker dominance index, *d*, as it is mathematically and conceptually simple (Southwood 1996) and characterises the distribution as well as, or better than, most other indices (May 1975). Here *d* was calculated for each insect species as the proportion of the most common plant interaction over all the interactions that the insect species made. Thus the index has the formula:

$$d = \frac{N_{max}}{N_t} \qquad \textbf{Equation 2.3}$$

where N_{max} is the abundance of the dominant plant species interaction and N_t is the total abundance of interactions.

I used repeated measures analysis of variance (Sokal and Rohlf 1995) to investigate the effect of meadow status (old or restored) upon plant and insect species richness, plant and insect species abundance, the proportion of plant species visited, and the number of pollen grains per insect. Where necessary, data were transformed to meet the assumptions of normality and the two missing samples from Meadow 2 were treated as missing values.

Kruskal-Wallis tests (Sokal and Rohlf 1995) were used to determine the impact of meadow status upon the median number of insect species visiting each plant species; the median number of plant species visited by each insect species; the median number of pollen species found on each insect species and the median number of pollen transporters per plant species. If a significant difference between the four meadows was found, an adaptation of the Tukey test was used to test for differences between the four meadows (Daniel 1990). Connectance and linkage density were compared among old and restored meadows in two-sample t-tests (Sokal and Rohlf 1995).The visitation webs were analysed using a Mantel test. A program written in SAS by Dr Eric Dyson was used for this test. A Mantel test is used to estimate the association between two independent matrices describing the same set of entities (here matrices of interactions between plants and pollinators) and tests whether the association between them is stronger than one would expect from chance (Sokal and Rohlf 1995). All four matrices were tested against each other.

2.3 RESULTS

2.31 Was the pattern of insect visitation similar for old and restored meadows?

The plants and insects found in the meadow are listed in Appendix C2 and the four visitation webs are shown in Figure 2.1 (old meadows) and Figure 2.2 (restored meadows). The purpose of these webs is to provide overviews of the quantitative differences between webs. It is apparent from the figures that there was much variation among the webs in terms of flower and insect abundance and general web structure. However, these differences were not clearly related to meadow status. Nor were there any systematic differences in the taxonomic structure of the insect assemblages in the two types of meadow: although there was considerable variation in the species composition on the four meadows, Diptera and Hymenoptera always dominated the insect community, both in terms of abundance and species richness. In both meadow types, the remainder of the flower visitors were Coleoptera, Lepidoptera and Hemiptera.

There was no systematic difference between old and restored sites in plant and insect species richness, plant and insect abundance, the number of flower groups, or in the proportion of plant species visited (Table 2.3). Pollinator generalisation appears to be the norm for plants in these communities, with mean and median values for the number of insect visitors being greater than one at each site (Table 2.4). There was no significant difference in the number of visiting insects at the four sites (Table 2.3). In contrast to plants, insect species appear to be more specialised, visiting a median of one species of plant (Table 2.4). There was no significant difference in the median number of plants visited by insects between the four sites.

The old meadows had a higher connectance than the two restored meadows, thus a higher proportion of potential links were realized. However, these differences were slight and could not be verified statistically (two-sample $t = 4.52$, $p = 0.069$). Connectance between insects and flower groups, as opposed to plant species, showed no obvious difference between old and restored meadows (Table 2.4). Nor was there any suggestion of differences in linkage density or in the Berger-Parker diversity indices (Table 2.4). This suggests that the insects divided their visitations between plants in a similar fashion in old and restored meadows.

The comparisons and Mantel test correlation coefficients for the visitation data between the pairs of meadows are shown in Table 2.5. All correlations were significantly (negatively) correlated ($p < 0.001$) at 20,000 randomisations. Thus each matrix is different from the other matrices, probably because of the low number of shared insect species at the four sites. The two least dissimilar meadows were an old meadow (Meadow 2) and a restored meadow (Meadow 4). In contrast, the two most dissimilar meadows were also an old meadow (Meadow 2) and a restored meadow (Meadow 3). This suggests that there are no systematic differences between old and restored sites. The simplest explanation accounting for these data is that all four meadows were structurally different from each other and that these differences were unrelated to their old or restored status.

2.32 Was the pattern of pollen transport similar for old and restored meadows?

Approximately 400,000 pollen grains were sampled from flower visiting insects at the four sites. Eighty-two percent of all insect specimens carried pollen from the plant species which they were caught on. The four pollen transport webs are shown in Figure 2.3 (old meadows) and Figure 2.4 (restored meadows). As before, the purpose of these webs is to provide overviews of the quantitative differences between the meadows. All four meadows depended heavily on Hymenoptera for pollen transport, and these insects transported 74% of pollen in the old meadows and 76% of pollen in the restored meadows (shown in black in the figures), respectively. This is greater than would be predicted on the basis of their abundance in the meadows (compare this data with Figure 2.1 and Figure 2.2, where Hymenoptera are shown in black). In both types of meadow the second most important group were the Diptera at 25% and 21%, respectively. Pollen transport by Coleoptera, Lepidoptera and Hemiptera made up a very small percentage of the total (Figure 2.5). The total number of pollen grains found on insect bodies was similar at the four meadows (Table 2.6). While the total amount of pollen being transported by insects was similar between the two types of meadow, the pattern of pollen transport over time was different. It was similar between the two restored sites but different between the two old sites (Figure 2.6). There was a significant difference in the Berger-Parker dominance indices among the four sites (Kruskal-Wallis $H = 9.14$, $p = 0.031$). However, looking at the mean index per site (Table 2.7) it is apparent that this difference is independent of the site status.

Generalisation appears to be the norm for both plants and insects, with all insect species carrying a median number of pollen grains greater than one, and all plants having more than

a single pollen carrier (Table 2.7). These data for insects contrast with the visitation data where many insects appear to be specialized. However, the pollen load is the better data as this provides a history of each insect's visitation. Therefore, it appears that the visitation data is underestimating the number of plant species visited. Connectance and linkage density were similar for the pollen data for Meadows 1, 3 and 4 and both for the species webs and the flower group webs. In contrast, Meadow 2 had a higher species web connectance and low linkage densities (Table 2.7). There were no systematic differences in either connectance or linkage density between old and restored meadows. However, when comparing these values between the visitation and pollen transport webs, the pollen transport webs always had significantly higher values (connectance, all species: two-sample $t = 9.26$, $p = 0.001$; connectance, flower group webs: two-sample $t = 5.03$, $p = 0.008$; linkage density, all species: two-sample $t = 6.71$, $p = 0.003$; linkage density, flower group webs: two-sample $t = 4.17$, $p = 0.013$). Thus, pollen transport webs are significantly more complex than visitation webs.

2.4 DISCUSSION

The plant-pollinator communities in the two types of meadow were very similar in plant and insect species richness, in the proportion of flower species visited by insects and in the numbers of pollen grains being moved by flower visitors. However, there was considerable variation in the species composition among the four meadows.

In this section I first discuss the structure of the plant-pollinator community at the four sites. Next I use the data to consider whether or not pollination processes have been restored successfully. I then discuss the advantages of studying interactions between species in restoration programmes. Finally, I outline the potential sources of bias in the study.

2.41 The structure of the plant-pollination communities on the four sites

The composition of the insect fauna was similar to that of the meadow described by Memmott (1999). Thus, Diptera and Hymenoptera were the most frequent flower visitors, with a small proportion of Coleoptera, Hemiptera and Lepidoptera making up the rest of the sample. In terms of the constituent species of both insects and plants, there was considerable variation among the four meadows, but the diversity of flower groups was similar among the meadows and made little difference to their analysis. Therefore, it is possible that hay meadow communities can be structurally very different but functionally quite similar.

The summary statistics from the webs can be compared to values in published visitation webs. The visitation connectance values lie between those for a Colorado web at 0.036 (Waser *et al.* 1996) and an average connectance reported by Jordano (1987) of 0.294. Thus, the values fall within the range of published values. In the study by Memmott (1999), plants were visited by a median of 7 species of insects (range 0-48) and insects visited a median of 3 species of plant (range 1-18). Here the values are lower as the plants at the four sites are visited by a median of 3, 5.5, 2 and 4 insects. The insect values are lower still as each insect species visited a median of 1 species of plant at each site. However, this is obviously an underestimate, as it is known from their pollen loads that they have visited a median of 3 or 4 plant species prior to being caught. These lower values are likely to be a consequence of the different sampling intensity in this work relative to Memmott (1999). Although the field season was longer in my study compared to the one month in Memmott

(1999), the transects used by Memmott (1999) were both longer than mine and sampled much more often.

While a few studies have looked at pollen loads in a flower visiting assemblage, these have previously been within a taxonomic subgroup of flower visitors, for example hawkmoths (Kislev *et al.* 1972), hoverflies (Haslett 1989) or hummingbirds (Feinsinger *et al.* 1987). I am not aware of any published studies describing pollen loads quantified for a whole community. When the connectance and linkage density values are higher for the pollen transport webs than those for the visitation webs, this is at least in part because the pollen transport data are summaries of several visitation webs and provide a history of past flower visitation. Visitation does not equate to pollen movement. For example, some interactions that occurred at high frequencies in the visitation web, occurred at low frequencies in the pollen transport web, or even failed to appear. Looking at the data overall, 18% of individual insects did not carry pollen from the plant species they had just visited. This is comparable with the 17% for insects on lowland heathland (Chapter 3).

2.42 The restoration of pollination processes

Mutualistic interactions, such as pollination and seed dispersal, presumably play a pivotal role in population establishment, reproduction, migration and community development (Montalvo *et al.* 1997). Leong (1994) reported that in a Californian pollination system consisting of andrenid bees and annual plants, visitation rates, numbers of taxa, and seed set were all lower in restored habitats in comparison with pristine habitats. This suggests that the restoration of pollination processes may not automatically follow the reinstatement of target plant species. In contrast, I found no significant differences in the functional biodiversity of plant and pollinators on the old and restored meadows, aside from a slight difference in visitation web connectance. However, there was considerable variation in the structural biodiversity.

Two values were calculated for visitation web connectance, one based on plant species and the second on flower groups. While the value based on flower groups showed no difference among old and restored meadows, the value based on species showed a statistically weak difference. If this reflects a true pattern, it suggests that the old meadows could have greater levels of ecological redundancy, i.e. more "spare species" in each functional group (Walker 1992). Here functional group would equate to flower groups and there is indeed a small difference between the two types of meadow, with old meadows

having a higher average number of plant species per flower group (2.4 vs. 2.0 species). Thus, while the insects can find the broad categories of plant that they need, there is less choice within each pollination class in the restored meadows. If this is the case, then it could have implications for the resilience of the system to species loss, because there will be a smaller pool of plant species remaining in restored habitats that can act as ecological equivalents for any plant species that becomes extinct. Even so, the meadow that was most species diverse was the restored Meadow 4 and it seems unlikely that there should be less redundancy on this meadow than on, for example, the less species-rich old Meadow 2. In a heathland fragmentation study, Webb and Hopkins (1984) found the highest number of insect species in small fragmented sites and attributed this to edge effects. It is conceivable that the small size of Meadow 4 leads to considerable edge effects and consequently a high species count for insects. Interestingly, Meadow 4 was in an urban area with a high density of gardens, thus the surrounding habitat matrix was likely to be good for pollinators (Owen 1991). However, the possibility remains that the species richness on Meadow 4 does not correlate well with ecological redundancy there, if the high number of insect species reflect a high influx of generalist species, which forage on the same types of flower. Thus flower species in e.g. Groups 4 and 5 might experience less redundancy than those on the old meadows. However, if this was true, it should have been reflected in the connectance for flower groups, which it was not. Moreover, Meadow 2 was mown early and therefore sampled less. It is plausible that the results for this meadow would have been more similar to the other old meadow, if Meadow 2 had not been mown so early.

Obviously, one problem in comparing restored meadows with old MG1 meadows is that it may never have been the specified goal to recreate MG1 type meadows on the degraded sites. Restoration schemes often aim at broader categories, such as 'hay meadows' or 'wildflower meadows', perhaps thereby indicating that restoration biologists are happy to see the meadow communities evolve and gradually find their own stable states. In the present study, the restored meadows could be regarded as richer versions of the MG1 community than were the old ones.

While there was no consistent difference in the quantity of pollen moved by insects at the restored and old sites, it is intriguing that the movement of pollen over time was similar in the two restored sites but very different in the two old sites (Figure 2.6). One possible explanation is that the restored sites are at a lower stage on the community development trajectory and the two sites have not had sufficient time to diverge.

Entomophilous flowers in temperate areas often have diverse pollinator faunas and are well buffered against a disruption in pollinator services (Bond 1994). This effect could be particularly evident in temperate meadow communities, since they experience a major disturbance annually, when they are mown. Consequently, pollinators have to either complete their pollen/nectar-feeding stage at that point or be able to switch to another habitat.

In conclusion, an important part of the pollination service, namely pollen transport by insects, has been successfully reinstated in the restored meadows. This alone does not equate to pollination but it is the obvious first step in constructing true pollination webs.

2.43 Use of species interactions in restoration ecology

There is a paucity of published restoration research that considers species interactions at the community level. One exception to this investigated the food web structure of a lake community where the top crustacean predator had become extinct, following the introduction of trout (McNaught *et al.* 1999). McNaught *et al.* (1999) reported on the reintroduction of missing components of their community and the subsequent recovery of the community. Their work illustrates an approach that could be used if vital links were found to be missing in plant-pollinator communities.

The use of a community level approach is increasing in applied ecology. Communities of interacting species have been used to investigate the impact of habitat fragmentation upon community structure (Kruess and Tscharntke 1994; Gilbert *et al.* 1998), non target effects in biological control (Henneman and Memmott 2001) and the impact of insecticide spraying on pest populations in rice ecosystems (Cohen *et al.* 1994). Reproductive mutualisms such as pollination and seed dispersal epitomize the subtle, complex web of interactions, which, if broken by human actions, could cause a cascade of extinctions (Bond 1994). Community level approaches such as the one described here can start to reveal whether restored sites are "working" from a pollination point of view. This approach provides data simultaneously on the two perspectives in any plant-pollinator interaction: on the food resource of the pollinator and on the pollination requirements of the plant.

2.44 Limitations in the construction of the webs

The results showed a remarkable similarity among old and restored meadows in several repects. This may reflect a successful outcome of these meadow restoration schemes.

However, the possibility remains that the methodology used was not rigorous enough to pick up the true differences among old and restored meadows, i.e. there was insufficient statistical power because of the small samples sizes.

While it would have been preferable to sample more than four meadows, food webs in general are rarely replicated (Cohen *et al.* 1993) due to the huge amount of work in their construction and restoration ecology in particular is subject to experimental design difficulties (Simberloff 1990b; Michener 1997). Therefore, the fact that the webs are replicated at all has been an improvement on traditional approaches! For example, it has shown that much variation can exist among reference sites belonging to the same habitat, thus illustrating the point that single sites may not be useful targets for restoration schemes. In Chapter 3, this replication issue is addressed by increasing the number of replicate sites.

Other limitations with the dataset are threefold. Firstly, I recorded only diurnal flower visitors, even though I was aware that night-flying moths were present at the sites. There are, however, practical problems associated with obtaining visitation data for moths. If a light is used, the moths are likely to be attracted from outside the meadows, but if a light is not used, they cannot be seen.

Secondly, I did not sample the small flower-visiting insects, which are found deep within the flowers, for example thrips and pollen beetles. Few pollination studies include these two groups, although they may be important pollinators (Hagerup 1950; Hagerup and Hagerup 1953; Ananthakrishnan 1993; Roubik 1993; Williams *et al.* 2001), especially when considering their high abundance.

Thirdly, it would have been ideal to sample more insects from each site: overall a total of 344 visitation interactions and 879 pollen transport interactions between plants and pollinators were recorded. While I sampled 78 insect species, 55 plant species and approximately 400,000 pollen grains, undoubtedly some rare interactions were missed.

In Chapter 3, I focus on heathland restoration schemes. The advantage of working on heathlands is that they are floristically simpler than hay meadow communities and, consequently, simpler to work with. It also means that we should be better able to pick up subtle differences relating to site history in a study of heathlands than in a study of hay meadows. Moreover, replication is more readily achieved in a heathland study for several reasons: firstly, because heathlands tend to aggregate in regions with similar conditions of soil and climate; secondly, because alternative land uses on these soils are economically unviable, heathland restoration is an attractive option; and thirdly, the heathland habitat has

a high conservation and restoration status because of the range of associated species that are only found there. Moreover, the restored heathlands in Chapter 3 share similar histories and were all restored in the early 1990s, in contrast to the meadows that were restored at different times and had different histories of degradation.

TABLES

Table 2.1 Four hay meadows in the Bristol area.

	Name	History	Grid reference	Size (ha)
Old meadows				
Meadow 1	Ashton Court Meadow	Ancient	ST 542 717	7.5
Meadow 2	Briery Leaze Meadow	Ancient	ST 601 681	2.5
Restored meadows				
Meadow 3	Ashton Golf Course	Restored early 1990s	ST 548 724	9.0
Meadow 4	Brandon Hill Wildflower Meadow	Restored early 1980s	ST 579 728	<1.0

Table 2.2 Flower group classification. The difference between an inflorescence classified as a 'single' flower or as 'many' flowers is defined in terms of whether medium-sized insects, such as hoverflies and honeybees, are able to walk rather than fly from one flower to the next, in which case the plant species is defined as having an inflorescence consisting of many flowers.

Flower group	Type	Inflorescence	Description
1a	Pollen flowers	Single	Easily accessible flowers, which produce pollen but no nectar.
1b		Many	Easily accessible flowers, which produce pollen but no nectar.
2a	Exposed / partly concealed nectar flowers	Single	Easily accessible flowers with exposed or partly concealed nectar. Mostly actino-morphic. E.g. *Ranunculus*.
2b		Many	Easily accessible flowers with exposed or partly concealed nectar. Mostly actinomorphic. E.g. all the Cruciferae and *Salix*.
3a	Concealed nectar flowers	Single	Nectar is concealed. E.g. *Geranium*.
3b		Many	Nectar is concealed in flowers united into heads. E.g. all the Asteraceae.
4a	Mechanical flowers	Single	Insects have to press open the flower to get the reward.
4b		Many	Insects have to press open the flower to get the reward in each flower of the flower head. E.g. *Trifolium*.
5a	Spur flowers	Single	Have nectar in deep and narrow tubes or spurs. The typical 'butterfly' flower.
5b		Many	Have nectar in deep and narrow tubes or spurs. The typical 'butterfly' flower.

Table 2.3 Basic statistics for the visitation webs.

	Plant species	Flower abundance	Flower groups	Insect species	Insect abundance	Interaction types	Proportion plants visited
Old meadows							
Meadow 1	26	121,381	7	37	101	69	0.39
Meadow 2	16	34,312	7	24	65	34	0.41
Restored meadows							
Meadow 3	28	31,650	6	28	72	40	0.30
Meadow 4	26	27,518	7	53	106	71	0.43

Table 2.4 Web statistics for the visitation webs. Shown Berger-Parker Indices are site averages.

	Insects / plant sp.		Plants / insect sp.		C species web	C flower group web	L species web	L flower group web	Berger-Parker Index
	Mean	Median	Mean	Median					
Old meadows									
Meadow 1	4.60	3	1.89	1	0.0717	0.2664	1.1129	2.1563	0.8309
Meadow 2	5.67	5.5	1.42	1	0.0885	0.2023	0.8500	1.4783	0.8824
Restored meadows									
Meadow 3	3.64	2	1.43	1	0.0510	0.2381	0.7143	1.1765	0.8851
Meadow 4	6.36	4	1.35	1	0.0515	0.1914	0.8987	2.1515	0.8816

Table 2.5 Significant correlation coefficients from Mantel analyses on the similarity of visitation patterns in the 4 meadows.

	Meadow 1	Meadow 2	Meadow 3	Meadow 4
Meadow 2	- 0.39153			
Meadow 3	- 0.42285	- 0.96965		
Meadow 4	- 0.41252	- 0.28354	- 0.32761	

Table 2.6 Basic statistics for the pollen transport webs.

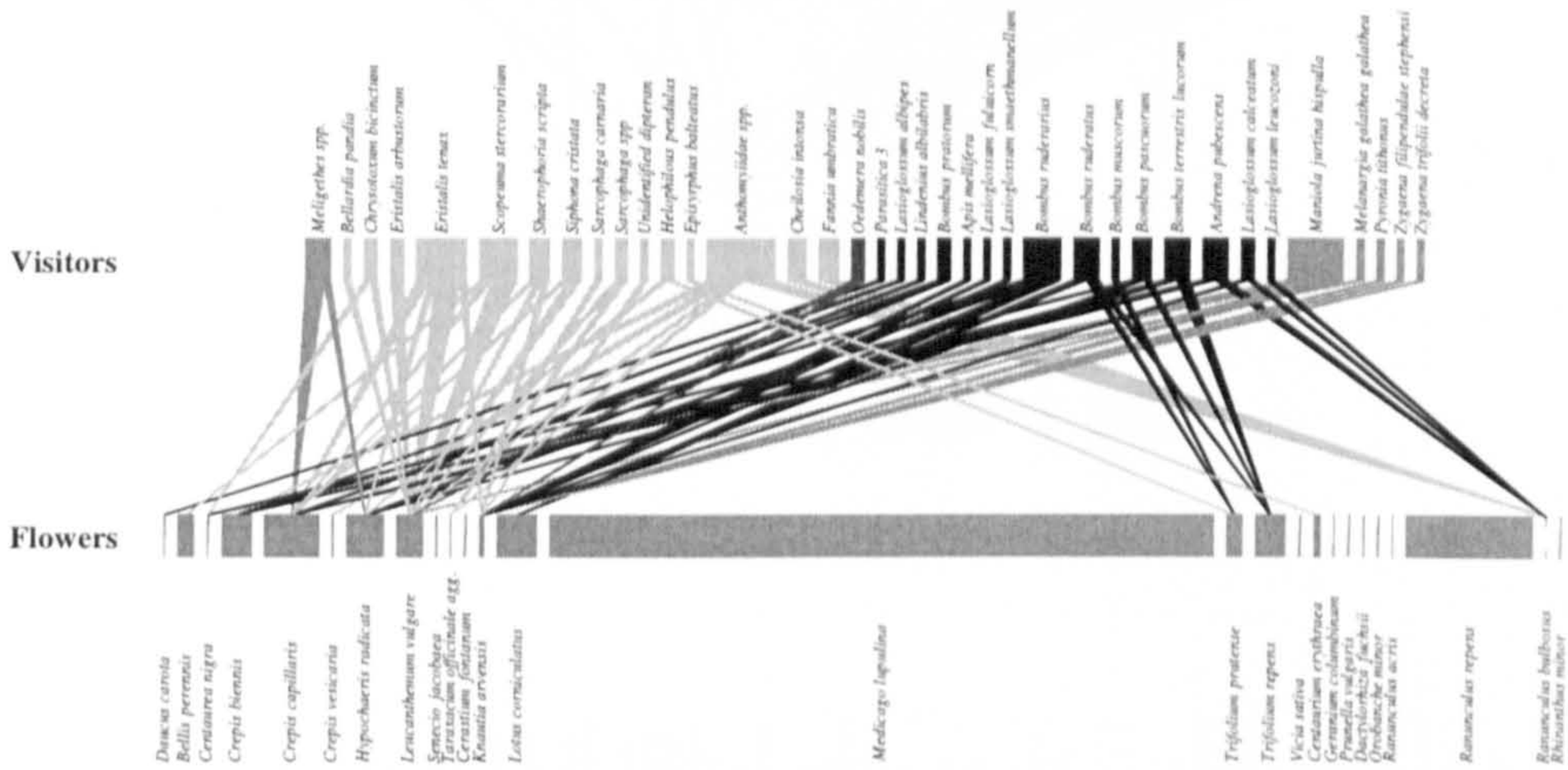
	Pollen groups	Pollen abundance	Mean number (range) grains per insect	Interaction types	Proportion plant species carried
Old meadows					
Meadow 1	20	106,055	1165 (0-12005)	185	0.95
Meadow 2	11	93,175	1579 (3-15763)	82	0.65
Restored meadows					
Meadow 3	18	86,231	1347 (0-17046)	168	0.72
Meadow 4	23	111,032	1122 (0-31956)	254	0.96

Table 2.7 Web statistics for the pollen transport webs. Shown Berger-Parker Indices are means per site.

	Median (range) carrier spp. / plant sp.	Median (range) pollen spp. / insect sp.	C species web	C flower group web	L species web	L flower group web	Berger-Parker Index
Old meadows							
Meadow 1	6 (1-32)	4 (1-13)	0.2500	0.3977	3.2456	4.2045	0.7554
Meadow 2	4 (1-22)	3 (1-8)	0.4583	0.3631	2.0000	2.6452	0.8428
Restored meadows							
Meadow 3	4 (1-13)	3 (1-11)	0.3333	0.3810	3.1698	4.9412	0.8472
Meadow 4	5.5 (1-25)	4 (1-14)	0.2084	0.3585	3.2987	4.2333	0.7238

FIGURES

(a) Meadow 1



(b) Meadow 2

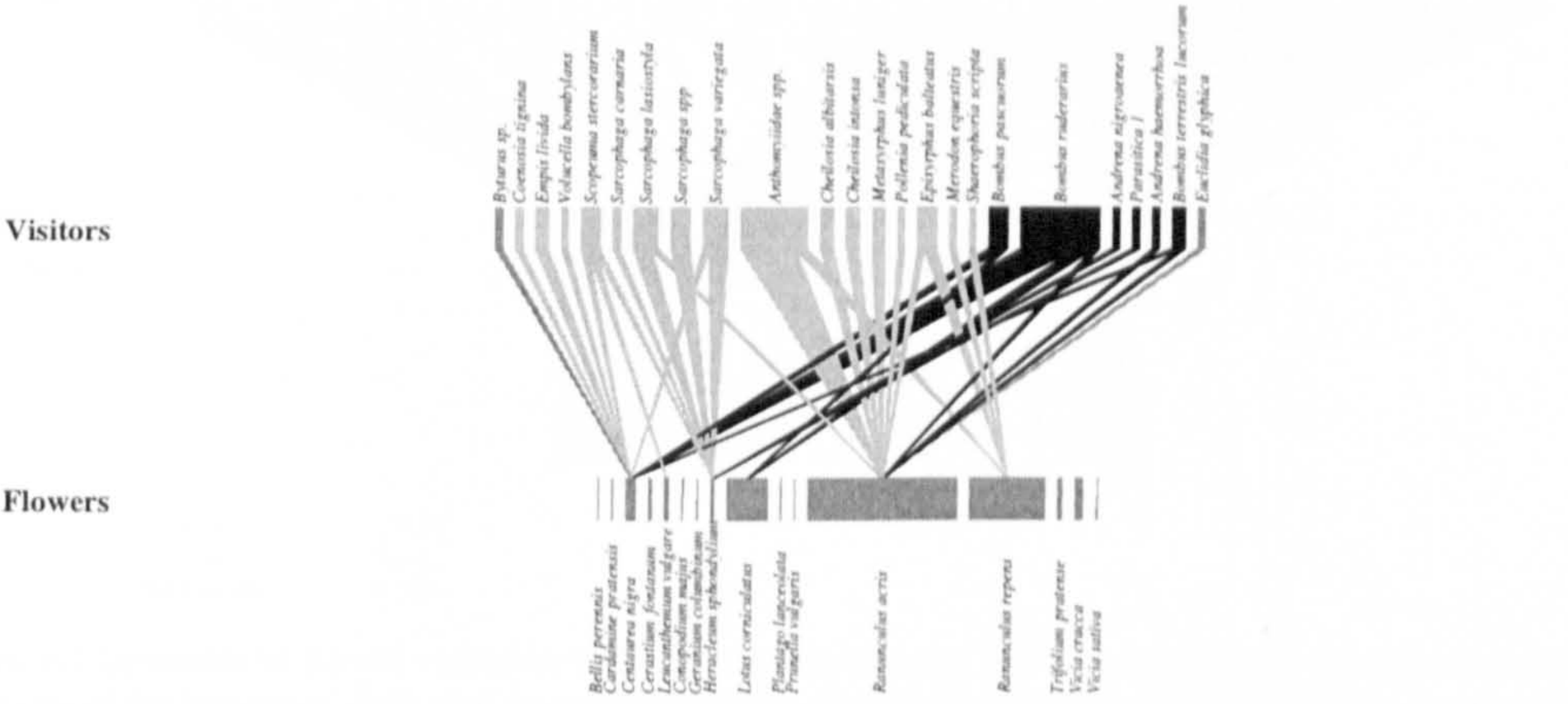
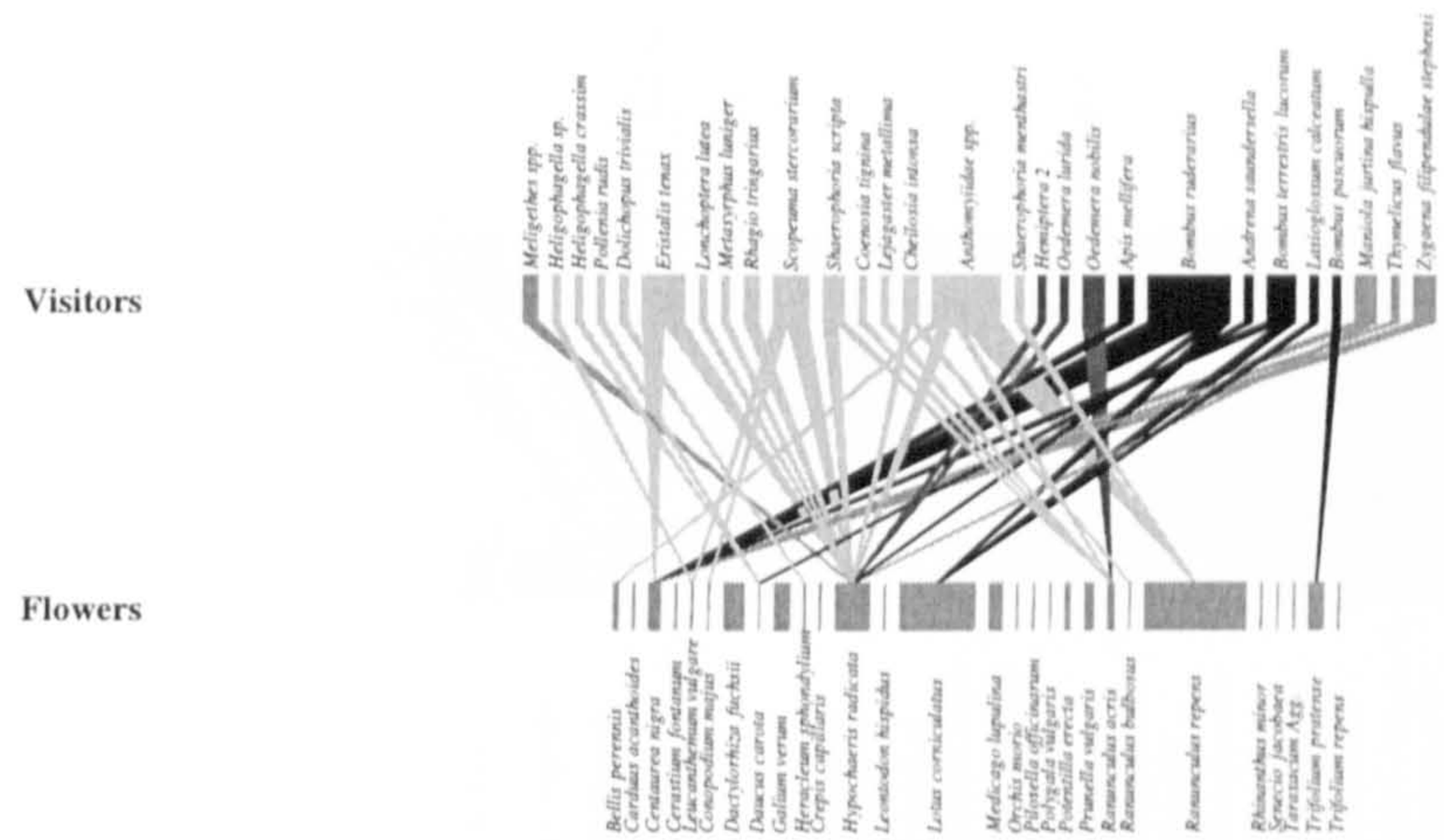


Figure 2.1 Quantitative flower visitation webs for the two old hay meadows. Plant species are shown as rectangles at the bottom of each web, insects are shown above and interactions link plants and insect visitors. The relative abundance of the species is indicated by the width of the rectangles and the frequency of each interaction type is indicated by the width of the line. Webs are drawn to the same scale as the webs in Figure 2.2.

(a) Meadow 3



(b) Meadow 4

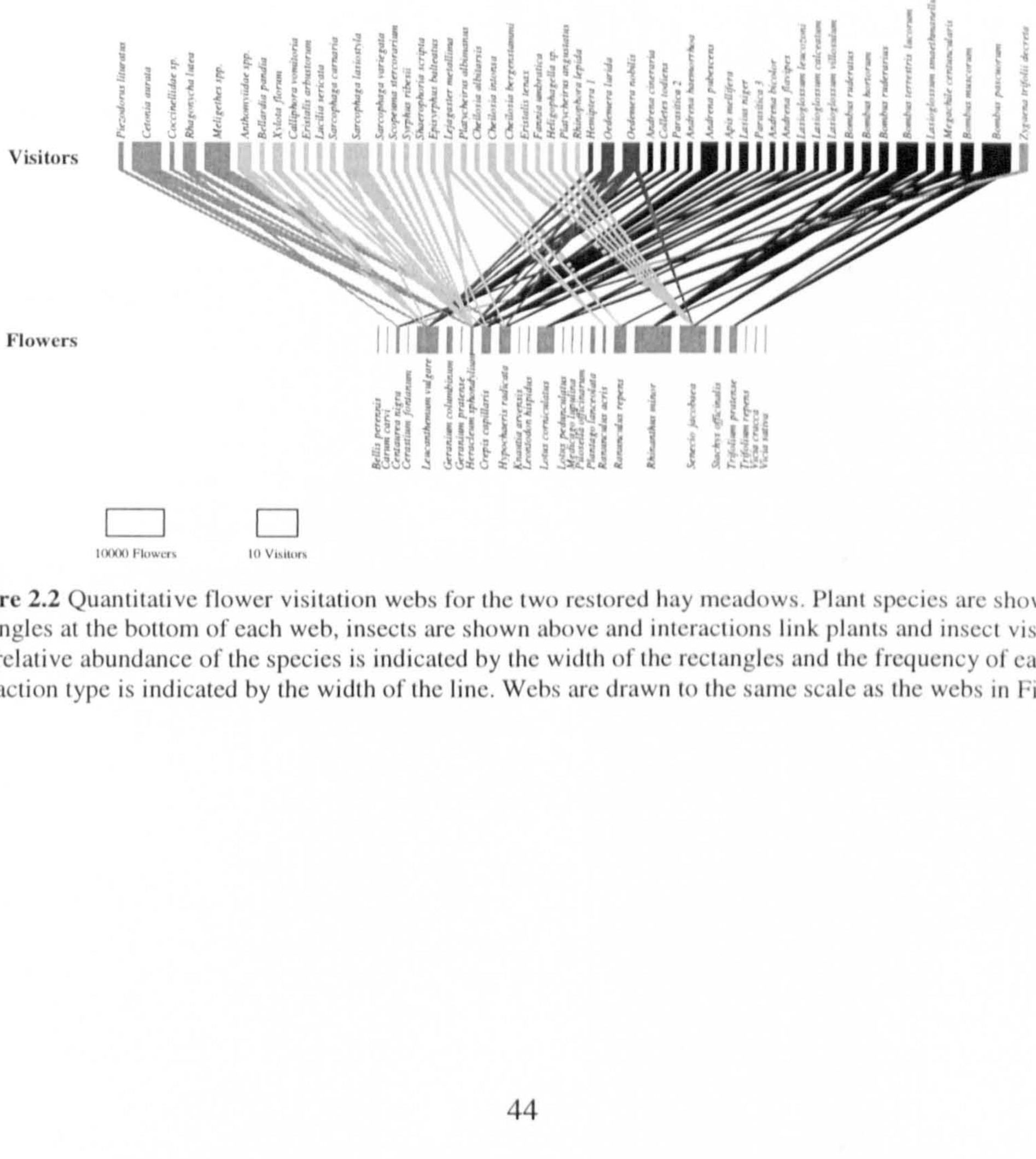
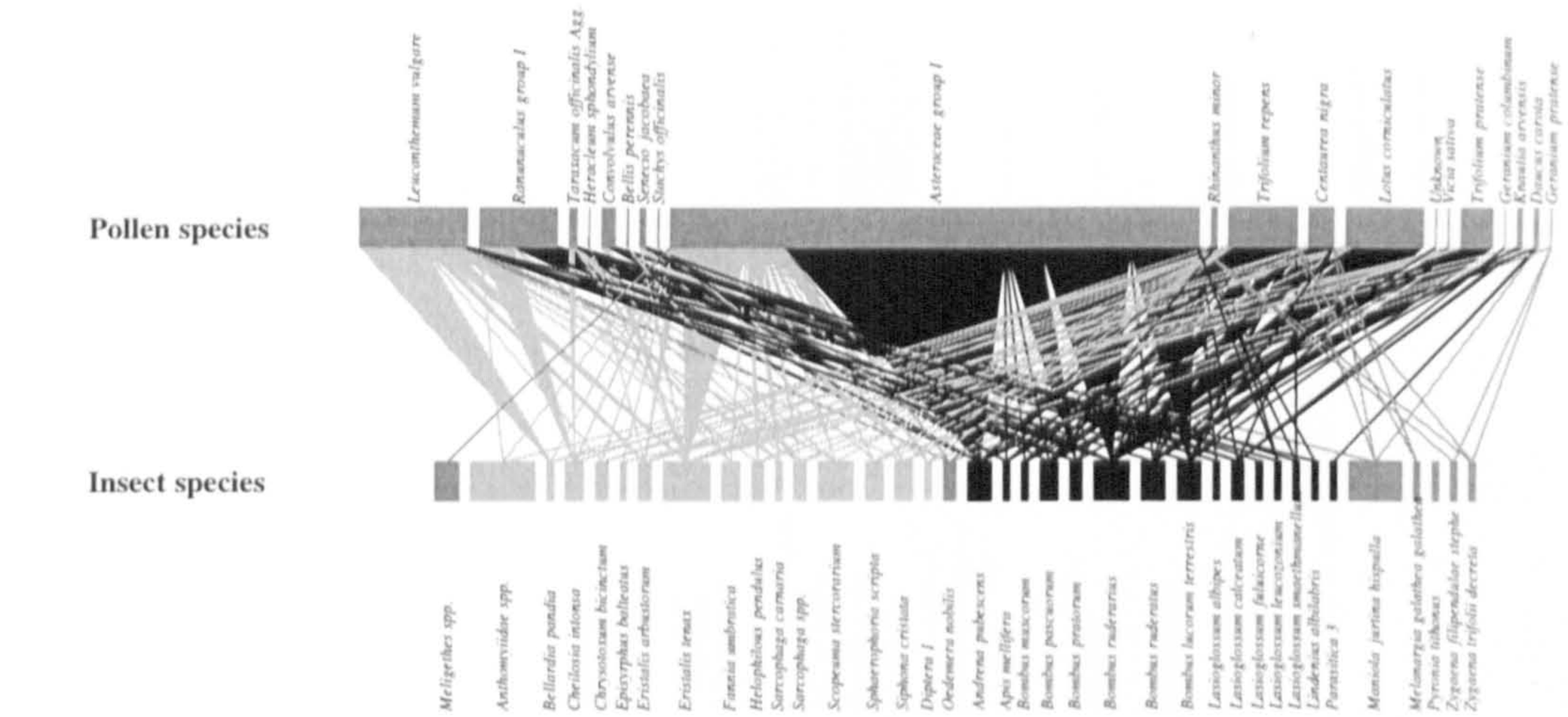


Figure 2.2 Quantitative flower visitation webs for the two restored hay meadows. Plant species are shown as rectangles at the bottom of each web, insects are shown above and interactions link plants and insect visitors. The relative abundance of the species is indicated by the width of the rectangles and the frequency of each interaction type is indicated by the width of the line. Webs are drawn to the same scale as the webs in Figure 2.1.

(a) Meadow 1



(b) Meadow 2

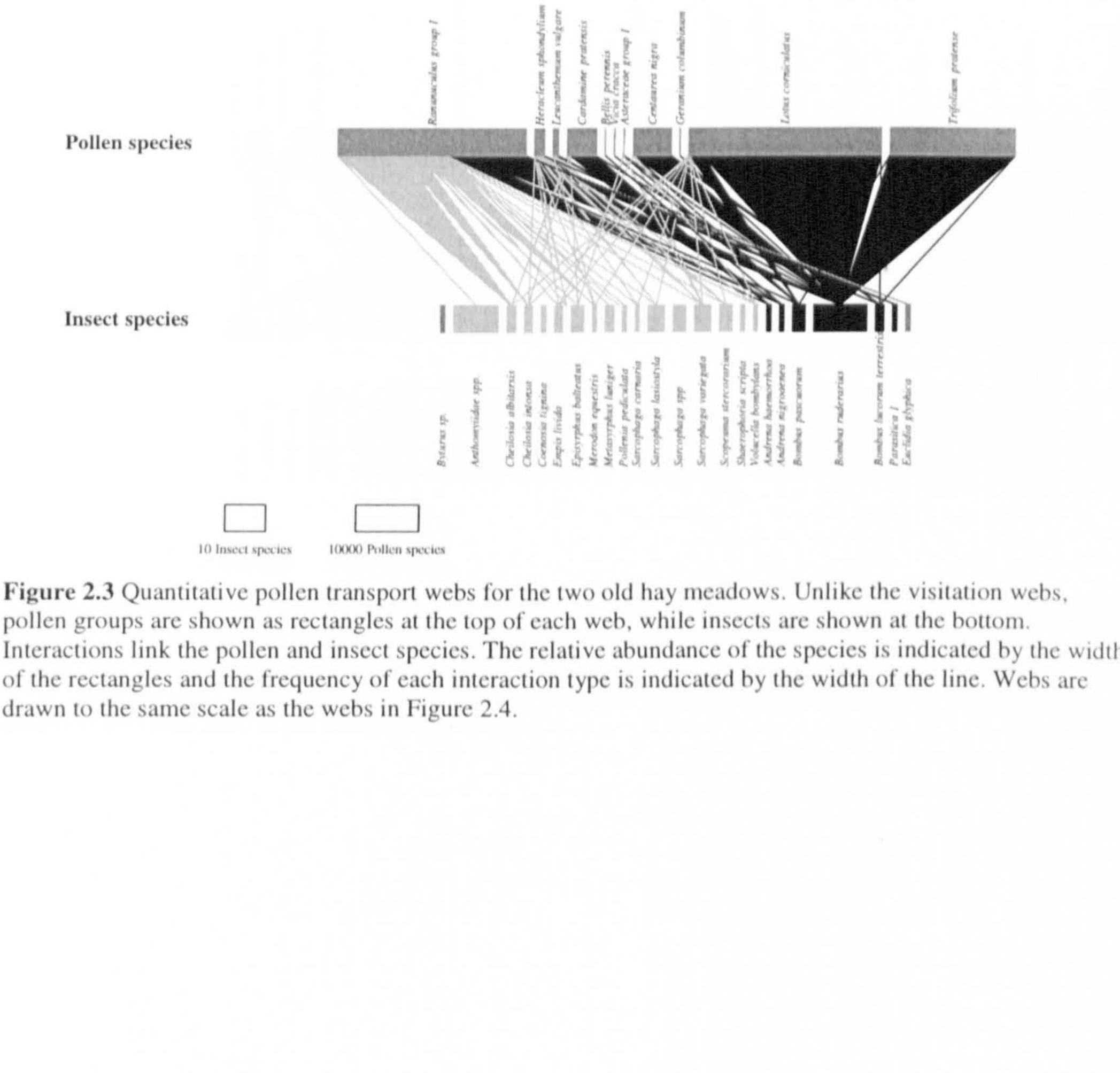
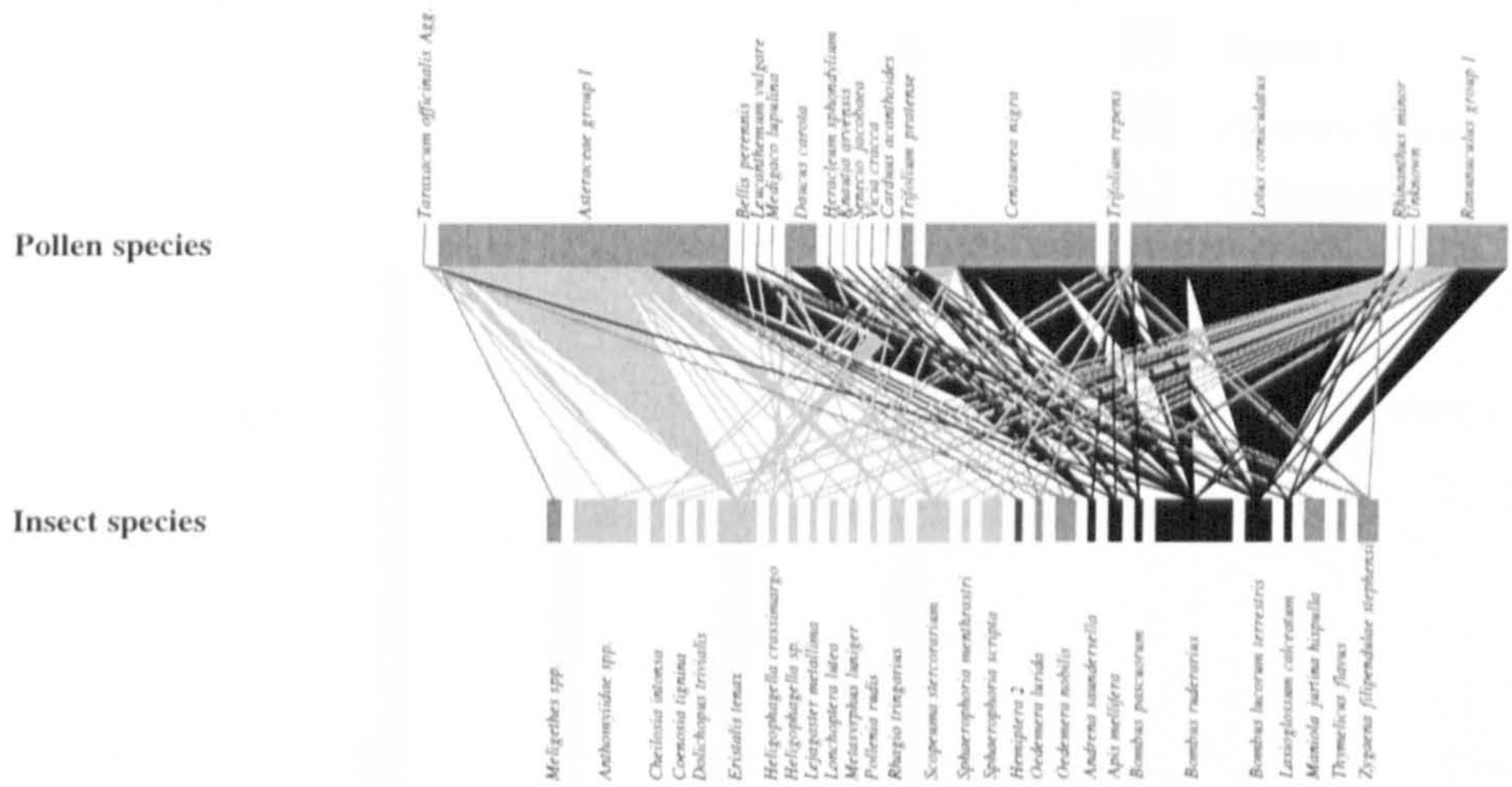


Figure 2.3 Quantitative pollen transport webs for the two old hay meadows. Unlike the visitation webs, pollen groups are shown as rectangles at the top of each web, while insects are shown at the bottom. Interactions link the pollen and insect species. The relative abundance of the species is indicated by the width of the rectangles and the frequency of each interaction type is indicated by the width of the line. Webs are drawn to the same scale as the webs in Figure 2.4.

(a) Meadow 3



(b) Meadow 4

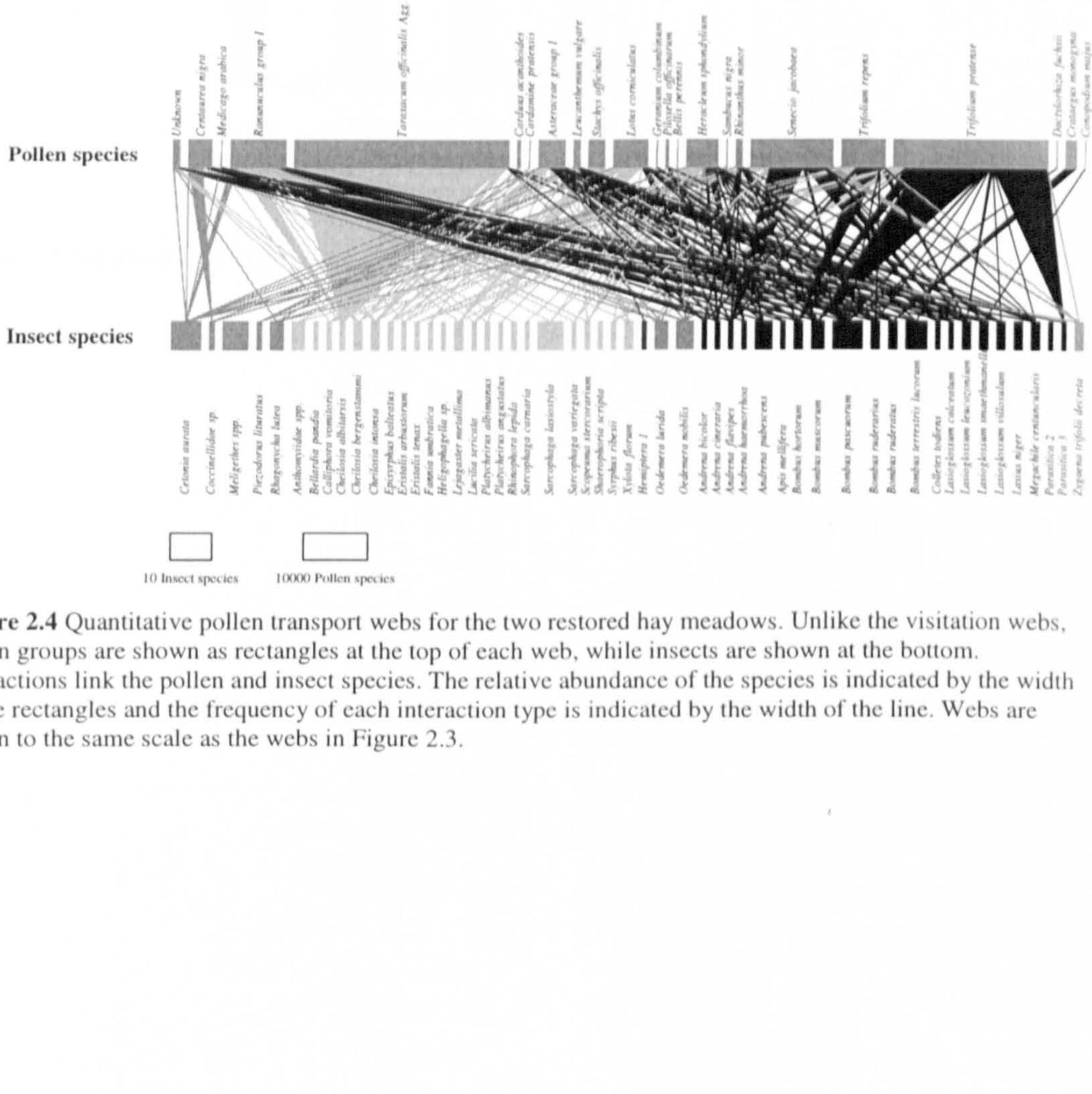


Figure 2.4 Quantitative pollen transport webs for the two restored hay meadows. Unlike the visitation webs, pollen groups are shown as rectangles at the top of each web, while insects are shown at the bottom. Interactions link the pollen and insect species. The relative abundance of the species is indicated by the width of the rectangles and the frequency of each interaction type is indicated by the width of the line. Webs are drawn to the same scale as the webs in Figure 2.3.

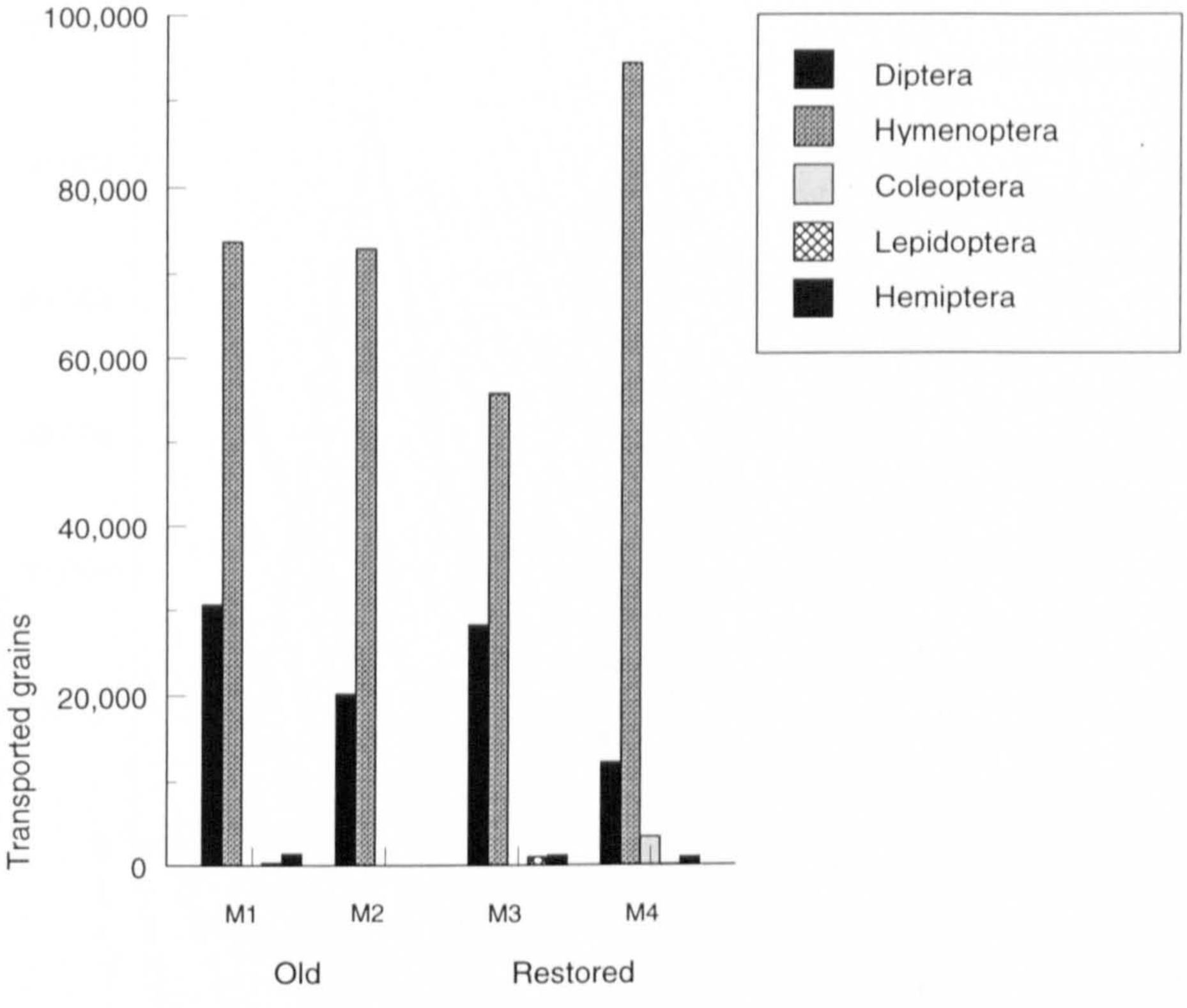


Figure 2.5 The abundance of pollen carried by the different orders of insect on the four meadows.

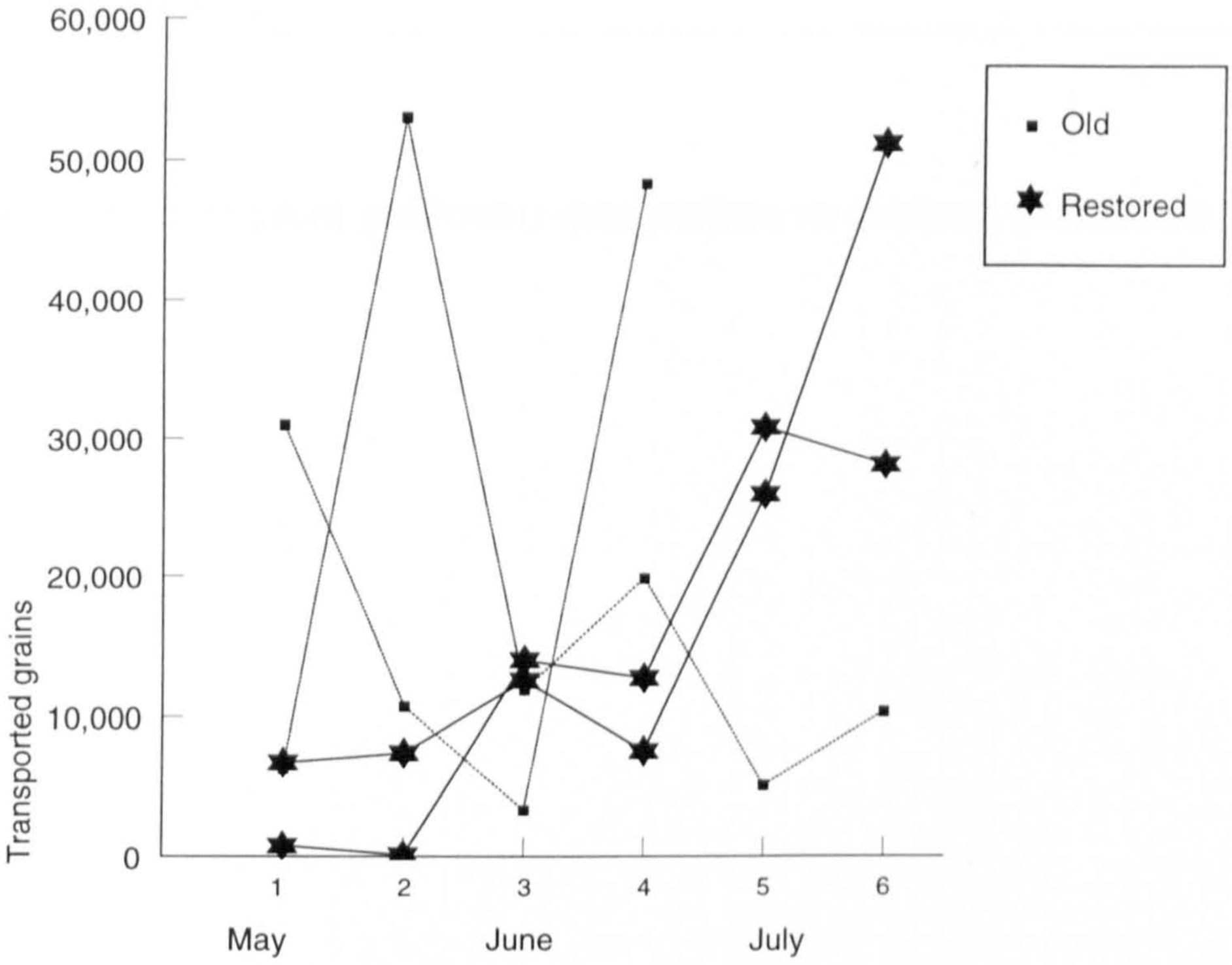


Figure 2.6 Pollen transport on the two old and the two restored meadows, respectively.

CHAPTER THREE

The restoration of plant-pollinator interactions on lowland heathlands

CHAPTER THREE

The restoration of plant-pollinator interactions on lowland heathlands

SUMMARY

Quantitative flower visitation webs and quantitative pollen transport webs were constructed for 4 pairs of old and restored lowland heaths in Dorset, England. The webs were compared in a variety of ways, with reference to both the structural and functional aspects of their diversity. Four models were constructed to account for the observed patterns: In Model 1 restored heaths were similar to adjacent old heathland, while in Model 2 they were similar to other restored heaths. In Model 3, restored heaths were similar to all other heaths irrespective of site history. In contrast, restored heaths would conform to Model 4 if they followed entirely idiosyncratic patterns. Evidence was found for all four models but most of it supported Model 2 and Model 3. On restored heaths Calluna vulgaris *dominated the flower community, whereas on old heathlands* Erica cinerea *was co-dominant with* C. vulgaris. *Because* E. cinerea *flowering peaked before that of* C. vulgaris, *the constancy of flower resources was reduced on restored heaths. Each heathland had a unique insect community, but functional biodiversity was similar on all heaths and restored sites fell within the range of natural variation of heathland communities. However, while quantitative pollen transport patterns were similar for old heathlands, restored heathlands showed no consistent trends. This is argued to be an artefact of the young age of these heathlands that will change as the restored heathlands mature.*

3.1 INTRODUCTION

3.11 Dry lowland heath

In Britain, dry lowland heath is an important focus for current conservation and ecological restoration work, partly because the habitat is associated with a number of rare or threatened species of vertebrates and invertebrates, and partly because Britain holds some 20% of the remaining European area of lowland heath (Michael 1996; Webb 1998).

Dry lowland heaths represent arrested succession; normally they require some form of human management to halt the secondary succession, which would otherwise turn them into woodland. This management is closely linked to the history of the heathlands, because they exist as a result of human activity. The dry lowland heaths developed some 4,000 years ago, when major forest clearances converted the land into an extensive agricultural system (Webb 1998). Through a combination of fodder cutting and grazing livestock, the nutrient status was reduced on the marginal soils. The livestock, which grazed the marginal land during the daytime, was kept near the farmstead at night, where their dung was collected and used for fertilising the better soils, where crops could be grown. Fire was sometimes used on the marginal lands in order to free up nutrients, which were trapped in the plant biomass, thereby encouraging new growth to the benefit of the grazing livestock. However, this further accelerated the nutrient loss from the marginal soils. Since the nutrient outflow was continually in excess of the inflow, the vegetation on these soils developed into a community of slow-growing, stress-tolerant species. The exact composition of these heathland communities would vary from locality to locality, in response to geology, local rainfall patterns, temperature range and variations in management (Rodwell 1991).

In the Poole Basin, Dorset, dry lowland heathlands are found on acid, predominantly free-draining soils. They are dominated by heather, *Calluna vulgaris* (L.) Hull, with other notable species being bell heather, *Erica cinerea* L., and dwarf gorse, *Ulex minor* Roth. Other frequent species are cross-leaved heath, *Erica tetralix* L., common gorse, *Ulex europaeus* L., and western gorse, *Ulex gallii* Planch. Most of the Dorset heathlands conform to the H2 (*Calluna vulgaris-Ulex minor*) heathland community in the National Vegetation Classification (NVC, Rodwell 1991), but where *Ulex gallii* occurs with *U.*

minor, the heathland is an intermediate type of the H2 and the H8 (*Calluna vulgaris-Ulex gallii*) communities.

The Dorset heathlands were once very extensive. A survey in the 1750s listed some 40,000 ha, but in 1978 only 6,000 ha remained (Webb and Haskins 1980; Rose *et al.* 2000). The majority of this loss was caused by afforestation, conversion to agriculture and urban spread (Rose *et al.* 2000). Over the past 20 years, most of the remaining heathlands have been afforded some protection and efforts have been undertaken to increase the overall heathland area. However, the heathlands are severely fragmented and many are completely enveloped by intensively managed land. Since the agricultural system, of which they once formed part, has disappeared, unhindered secondary succession is therefore currently the greatest threat to the remaining heathlands (Webb 1998).

3.12 Heathland pollinators

Although the heathland vegetation is species poor, the pollinator community can be very diverse, and include rare species, such as the UK biodiversity action plan (BAP) species the silver-studded blue butterfly, *Plebejus argus* L., and the brown-banded carder bee, *Bombus humilis* Illiger (Anon. 2000). However, the majority of heathland pollinators are species which are not necessarily restricted to this habitat. They include many species of bumblebee, hoverflies and other flies (Colyer and Hammond 1968; Stubbs 1983; Benton 2000). Likewise, honeybees, *Apis mellifera* L., are commonly found on heathlands, because heathland honey is considered of high quality and because bee keeping has historically been a way to earn an income from the heathland (Butler 1974).

3.13 Heathland restoration

Heathland restoration is a well-documented practise in Britain and elsewhere (Lowday and Marrs 1992; Marrs *et al.* 1992; Aerts *et al.* 1995; Pywell *et al.* 1996; Mitchell *et al.* 2000). In common with hay meadow restorations, the soil nutrient status is particularly important in determining the successful outcome of a heathland restoration scheme. Arguably, the most favourable site for heathland restoration is where the original heathland was replaced by pine (*Pinus* spp.) woodland either by deliberate plantings or through unhindered secondary succession. In such situations, not only will soil disturbance normally have been negligible, at least following the initial disturbance in the case of planted woodlands, in common with the ericaceous shrubs of the heathland, the acidic pine litter will not have

increased the fertility of the soil (Mitchell *et al.* 1997; 1999; Mitchell *et al.* 1998; Mitchell *et al.* 2000). To my knowledge, the majority of heathland restoration schemes in the Poole Basin are carried out on sites which earlier supported a pine cover.

I am not aware of any heathland restoration schemes which have considered pollinators. However, in order for a restored heathland to be sustainable in the long term, sexual reproduction of the plant community has to be reinstated (Neal 1998). Moreover, the restoration of biodiversity could have important implications for ecological functioning (Lawton 1994; Naeem *et al.* 1995; Hector *et al.* 1999; Tilman 1999; Hector *et al.* 2000). For example, biodiversity has been found to increase drought resistance and productivity in grasslands (Tilman and Downing 1994; Hector *et al.* 1999). It is plausible that also pollination increases as the number of insect species increases. Moreover, some redundancy may be a characteristic of healthy plant-pollinator systems, as this increases the likelihood of pollination even when sub-optimal conditions cause some pollinator species to decline. Therefore, populations of several pollinating species must be present on restored heaths. The reason why so little attention is traditionally paid towards this important aspect of restoration may partly be an assumption that pollinators can find their own way onto restored sites, but it could also betray a bias towards the conservation of other groups of species, such as rare plants, birds and lizards.

3.14 Heathland study sites

Compared to the hay meadows in Chapter 2, lowland heaths are ideal study sites for ecologists interested in restoration projects because: 1) since they are poor in plant species, heathlands may sooner achieve an acceptable degree of restoration compared with other habitats, such as hay meadows; 2) a restored site is normally found close to old heathland and this is thought to speed up the restoration by minimising the distance which colonising species have to travel, and also provides a target (the old heathland) with which to compare the restored site; and 3) since lowland heaths tend to be concentrated in places with similar climate and soil types, a number of restored sites may be found in the same area that can act as replicates.

3.15 Plant-pollinator interactions on old and restored heathland

This chapter describes a study which was carried out over the eight months from April to October 2001 on 4 pairs of old and restored dry lowland heaths in England. The objectives

of the study were three-fold: 1) to construct quantitative flower visitation webs and quantitative pollen transport webs for each heathland; 2) to compare and contrast the heaths in terms of both the structural and functional aspects of their biodiversity; and 3) to use these data to evaluate the success of the restoration schemes. For the purposes of comparing restored and old heathlands, four models were developed to account for the observed patterns.

3.2 METHODS

3.21 Study sites

Plots were established on 4 pairs of dry lowland heath in the Poole Basin, Dorset (Figure 3.1). Table 3.1 lists the location and approximate sizes of these 8 sites. All are found within a 100 km^2 area with a uniform climate and soils. Three of the pairs consisted of an old heathland with an adjacent restored heathland, but the fourth pair, Gore Old and Holton Restored, were separated by 3 kilometres. However, Holton Restored was found adjacent to old heathland, but access was not granted to this site because it is severely polluted with asbestos. Gore Old was the next nearest site of old, accessible heathland. Six of the heathlands were managed and grazed by livestock. The remaining two, Hyde Old and Hyde Restored, were not grazed during the study, but some mowing occurred on Hyde Old.

The four restored sites shared a similar history. Their original heathland communities were lost to conifer plantations between 1950 and 1970, but these were cleared in restoration projects between 1990 and 1992. At Holton Restored, the restoration effort involved only the removal of cut stems and branches, while brash was burned at both Hyde Restored and Morden Restored. At the smaller Hyde Restored, this had happened in various places inside the sampling plot, whereas on Morden Restored it took place outside the sampling plot. Arne Restored was faced with invasion by bracken, *Pteridium aquilinum* (L.) Kuhn, in the first year following pine clearance. Hence topsoil was scraped off to remove bracken rhizomes on this heathland (J. Day, RSPB officer, *pers. comm.*).

3.22 STUDY 1: *quantitative flower visitation webs*

Data were collected on 8 occasions, every three weeks from April until September 2001. At each site a circular plot was established (200 m diameter) and marked with a wooden pole at the centre. Over the season, sites were alternately sampled in the morning and in the afternoon in order to avoid differences emerging between sites that reflected patterns in insect day activity rather than true site differences. When sampling, two 2 m x 100 m transects were laid out in a random direction from the wooden pole. Each transect was sampled twice in the same way as the hay meadows in Chapter 2.

Following the sampling of flower visitors, the identities of all flowering, entomophilous plant species which grew in each transect, were recorded with their abundances. The

copious flowering of the ericaceous shrubs in July, August and September meant that counting individual flowers was unrealistic. The abundance of these species was therefore estimated from six 1 m quadrats placed along the transect line at the 15 m, 30 m, 45 m, 60 m, 75 m and 90 m marks. Plant species not found in transects, but growing elsewhere on the site, were also recorded but their abundances were not quantified. All sampling was carried out in calm, dry weather with temperatures at or above the average for that day.

With assistance from taxonomists at the National Museum of Wales, almost all insects were identified to species, although some specimens could only be identified to the level of genus, while a few were morphotyped. Workers of *Bombus lucorum* L. and *Bombus terrestris* L. are very difficult to tell apart and these species were therefore grouped as *Bombus lucorum/terrestris*, similar to Dicks *et al.* (2002). The visitation data were pooled across transects and sampling dates and used to construct quantitative flower visitation webs in the style of Memmott (1999). Similarly to Chapter 2, these webs, which were drawn by Dr Jane Memmott with a programme written in Mathematica™, show the abundance of both flowers and insects, as well as the frequency of their interactions.

3.23 STUDY 2: *quantitative pollen transport webs*

A pollen reference collection of all flowering entomophilous plant species, encountered in or around the heathlands at any one sampling event, was made similar to the method in Chapter 2. This collection was used to produce a key for the subsequent pollen analysis.

In the laboratory, each insect specimen was carefully sampled for pollen. Only the left side of the insect in the vertical plane was sampled on both the dorsal and ventral surfaces. By doing this, all potential pollen-carrying surfaces were sampled whilst the amount of pollen collected for microscopy was reduced by fifty percent. Surfaces were sampled using a small square of fuchsin pink staining gel held by a pair of forceps, similar to the method in Chapter 2. Pollen was identified under the light microscope using the key plus Erdtman *et al.* (1961; 1963). Some sub-sampling was carried out on the abundant *Apis mellifera* and *Bombus lucorum/terrestris*. If a high number of bees belonging to one of these species was caught on the same day and heathland, in the same transect and on the same flower species, only the first 8 individuals were sampled for pollen, and their average pollen load used to estimate that of additional individuals. Interactions with fewer than 5 pollen grains were not included in the analysis, because of the increased likelihood that small pollen loads were

caused by contamination. The resulting data were used for constructing quantitative pollen transport webs, similar to the ones in Chapter 2.

3.24 Four models for heathland restoration

Four alternative models were developed to account for the structural and functional biodiversity of the four restored heathlands. Model 1: restored heathlands were more similar to adjacent old heathland than to old or restored heaths further away; Model 2: restored heathlands were more similar to other restored heathlands than they were to old heathlands; Model 3: restored heathlands shared similar structural and functional biodiversity with all other heathlands, irrespective of whether they be old or restored heathlands; and Model 4: restored heathlands developed idiosyncratically; there were no consistent trends and similarities to restored or old heathlands had arisen entirely by chance.

Because heathland restorations are normally carried out near existing heathland, Model 1 may intuitively be the most likely scenario. Individuals from adjacent old heathland are more likely to colonise a restored site than are individuals from sites further away, and the resulting community should therefore resemble the structural biodiversity of the adjacent old heathland. Indeed, this is the underlying rationale for restoring heathland in close proximity to old heathland. If species behave in similar ways on both sites, the two sites should also be comparable in terms of their function. However, the time scale for this to be detectable could be considerably longer than the 10 years given in the present study. Although there may be a constant flow of species from the adjacent old heathland onto the restored site, many of these species will fail to establish if site conditions are still unfavourable to them. Moreover, the species which do establish could behave differently on the new heath, e.g. in the absence of a competitor or a predator. Therefore, a restored heath could be more similar to other restored heathland, as predicted in Model 2: although a restored site may receive most colonists from adjacent old heathland, a similar screening process exists on all restored sites, whereby the same kinds of organism are favoured. For example, if a species of *Bombus* prefers to nest in lichen and moss, this species may not be able to locate a suitable nesting site on a 10-year-old restored heathland, where lichen and moss have yet to build up. Rather it will be the species with a broad tolerance to site conditions that are favoured. However, this assumes that restored sites receive the same range of colonisers and, hence, that old sites are also similar to each other. Since these have

had very long time to diverge, this may not be the case. Instead, Model 3 could apply: given the constraints of heathland management, all sites share a fundamental structure but, apart from this, each site follows a unique cycle or trajectory, depending on the microclimate, the distance to source populations, the sequence of species establishment, etc. (Drake *et al.* 1993; Luh and Pimm 1993; Law and Morton 1996). In extreme cases, restored sites could show little sign of following a predictable trajectory towards complete heathland restoration and would therefore conform to Model 4: similarities to other heathland sites are entirely accidental and follow no predictable trends. For example, if bracken had been allowed to invade Arne Restored, this could have had dramatic effects on the trajectory of this site. Bracken has been found to increase the soil fertility on heathlands (Snow and Marrs 1997) and could entirely prevent the establishment of the heathland community. However, the bracken invasion case also serves to illustrate that Model 4 is an unlikely scenario, since both the restoration and heathland management programmes will normally prevent restored sites from following entirely idiosyncratic pathways.

3.25 Statistical analysis

Webs were compared in several ways. First of all, structural aspects of the web diversity were compared across the 8 heathlands. This included species counts and the Shannon-Weaver diversity index, H' (Shannon and Weaver 1963), which was complemented with 'evenness', the fraction of H' over ln$S$, where S is the total number of species in the sample (Pielou 1975). Thus an evenness close to 0 means that species abundances differ greatly, while values close to 1 means that they are very similar. Distributions of species and insect groups were compared in Chi-square analyses. Insects were grouped into Coleoptera, Diptera excluding Syrphidae, Syrphidae, social Apidae, solitary Apidae and 'other insects'. However, as it is debatable whether social insects are statistically independent (Fowler and Cohen 1996), these were considered separately. Secondly, analysis considered the functional aspects of the biodiversity among the 8 sites. Here both taxonomic and trophic species concepts were employed. A trophic species is defined as a 'group of organisms which behave in a functionally similar way (Briand and Cohen 1984). Thus in the quantitative visitation data, one or more taxonomic species were grouped into one trophic species if they showed the same range of visited plant species, although relative differences in the frequency of visits to each plant species were ignored. These groupings reflected the

qualitative species behaviour in each type of web and different groupings could therefore arise amongst the quantitative flower visitation and pollen transport webs.

In addition to linkage density, L, which is the average number of observed linkages per species, two measures of connectance, C_r and C_d, were employed to describe the complexity of the webs. The first of these was the realistic measure, which I used in Chapter 2:

$$C_r = \frac{l}{IP} \qquad \textbf{Equation 3.1}$$

where l is the number of observed linkages, I is the number of insect species and P is the number of plant species. Thus C_r is the fraction of possible linkages that has been realised. The second measure, C_d, directed connectance (Martinez *et al.* 1999), follows the formula:

$$C_d = \frac{l}{S^2} \qquad \textbf{Equation 3.2}$$

where S is the total number of species in the sample. Clearly, in a web such as a flower visitation web, C_d can never attain unity, as this would mean that not only were all insect species visiting all plant species, they were also visiting all insect species, including themselves, and the plant species were visiting all insect and plant species including themselves. However, the measure has been demonstrated to be valid when comparing trophic species webs of different sizes (Martinez 1992; Martinez *et al.* 1999). Figure 3.2 shows the potential distribution of IP and S^2 in samples with 1 – 10 plant species and 1 – 50 insect species. The figure illustrates the sensitivity of C_r to the addition of extra plant species compared with C_d. As more species are added to a web, distinct isobars emerge for each number of plant species in C_r. As a consequence of this sensitivity, C_d may be the better measure when comparing web complexity across the 8 sites.

Other comparisons included insect-plant ratios, i.e. the number of insect species divided by the number of plant species, as well as the fraction of specialist species in the insect community, since this could reflect the maturity of the heathlands. Old heathlands may include more specialist species, because restored heathlands may not yet have reached the stage where a varied diversity of insect types can persist over time (Waser *et al.* 1996; Kearns 2001). The degree of generalization in both the plant and insect communities was compared among old and restored heathlands in terms of the mean and median number of insect species that each plant species interacted with and the number of plant species that

each insect species interacted with. These values were subsequently compared in two-sample t-tests (Sokal and Rohlf 1995).

The number of "spare" pollinators in each web was also compared among the 8 heathlands. Increased redundancy is thought to increase ecosystem stability, because adverse events are unlikely to affect all species equally severely (Lawton 1994; Palmer 1997; Kearns 2001). Paired t-tests (Sokal and Rohlf 1995) compared the number of interacting insect species for each plant species, which a given combination of two webs had in common.

Using a programme written by Adam Liedloff (Mantel Shareware Version 2.0), Mantel tests were used to compare pairs of webs with respect to shared plant species and their interactions with insects. In these Mantel tests two dissimilarity half-matrices were compared by calculating a test statistic, *Z*, based on same-cell multiplications between the two matrices (Mantel 1967). In the dissimilarity half-matrices, cells were the fractions of insect species that interacted with just the one plant species in each combination of two plant species, divided by the total number of insect species interacting with the two plant species. Therefore, these Mantel tests allowed for a comparison of the pattern of interactions in two webs. Matrices were drawn up and compared for both the visitation and the pollen transport data. The latter analysis was separated in two: 1) the abundance of pollen carriers, i.e. the number of insect species observed to carry the pollen of just one species in a given combination of two plants; and 2) quantitative pollen transport, i.e. the amount of pollen that those insects carried divided by the total amount of pollen between the pair of plant species. If pollen carrier abundance was similar for a given pair of webs, but quantitative pollen transport was not, it would mean that species behaved differently in the webs. Because rare pollen species can increase the probability of an association between two dissimilarity matrices, only the most widespread pollen species were considered in these two analyses, i.e. *Calluna vulgaris*, *Erica cinerea*, *Erica tetralix*, *Ulex europaeus* and *Ulex minor*.

3.3 RESULTS

3.31 STUDY 1: *quantitative flower visitation data*

The 8 quantitative flower visitation webs are shown pair-wise in Figure 3.3 – Figure 3.6. These webs are drawn to the same scale and provide comparable overviews of the data. The basic web statistics are summarised in Table 3.2.

3.32 Entomophilous flower species

Thirty-one species of plant were recorded in the study, of which only 15 grew in the transects (Appendix C3). The restored heaths contained more plant species than the old heathlands (Figure 3.7), but many of these extra species were ruderals, such as *Cerastium fontanum* Baumg. and *Taraxacum* Agg. Wigg. (Grime *et al.* 1988). The characteristic heathland species were found on all the heaths. These included the 'core' species, *Calluna vulgaris*, *Erica cinerea*, *Erica tetralix*, *Ulex europaeus* and *Ulex gallii/Ulex minor*. Flower abundance is shown in Figure 3.8. *Calluna* was the most abundant flower species on all heathlands, and more abundant on restored heaths than it was on old heathlands (two-sample $t = -1.92$, $p = 0.048$). In contrast, *E. cinerea* was more abundant on old heathlands than on restored heaths (two-sample $t = 2.28$, $p = 0.028$). Because *E. cinerea* flowering peaked before *Calluna* flowering, restored sites had fewer flowers early in the summer, but more flowers in late summer. These seasonal differences were significant (Repeated Measures ANOVA, $F_{(1,6)} = 104.41$, $p < 0.001$).

3.33 Insect community structure

One hundred and twelve species of insect were found overall. Fifty-one of these were recorded on only one heathland with a single individual, while a further 23 species were recorded on two or more heathlands but with only a single specimen per heath. Eighty-six insect species were recorded on old heathlands, 13 of which were not found on restored heaths. Seventy-four species were recorded on restored heaths, 8 of which did not occur on old heathlands. Only 5 insect species were common to all 8 heathlands. The species are listed in Appendix C3, together with the sites where they were found.

Insect diversity was always higher on the old heathland within a given pair (two-sample $t = 4.36$, $p = 0.011$), but considerable variation was found among pairs (Table 3.2 and

Figure 3.7). Figure 3.7 clearly illustrates the value of a paired design: although considerable variation exists among pairs, trends are consistent within pairs. The Shannon-Weaver and evenness indices showed no consistent trends within or between pairs. Table 3.3 lists the similarity of the heaths in terms of the proportion of shared insect species. The maximum similarity was comparable across all sites, ranging from 54% to 68%. Restored heaths showed no consistent trends in similarity, and only Hyde Restored was most similar to adjacent old heathland. Old heaths shared similar proportions of species with both old and restored sites, although in absolute terms they had most species in common with other old heathlands.

A total of 2723 insect flower visitors were sampled. There was a trend of higher insect abundance on old heathlands, although this was statistically weak (old heathlands, $\bar{x}$ = 400.75 (median = 394.5); restored heathlands, $\bar{x}$ = 280.00 (median = 281.5), Mann-Whitney U = 1.50, p = 0.059). Total insect abundance was not significantly related to total flower abundance (Pearson r = 0.43, p = 0.281).

There was no significant difference in the number of species within each insect group, neither when pooling the heathlands into old vs. restored sites (χ^2 = 3.84, d.f. = 5, p = 0.568) nor when comparing the 8 sites to each other (χ^2 = 20.29, d.f. = 28, p = 0.853). Likewise, the number of *Bombus* species was similar among old and restored heaths (Mann-Whitney U = 6.00, p = 0.691).

However, the relative abundance of the insect groups, in terms of insect numbers, varied among the heathlands. When grouping sites as either old or restored, solitary bees were positively associated with old sites, while Coleoptera were positively associated with restored sites (χ^2 = 21.69, d.f. = 4, p < 0.01). However, when analysing sites individually, only Arne Old and Gore Old showed positive associations with solitary bees, whereas Hyde Old and Holton Restored both showed a negative association (χ^2 = 83.12, d.f. = 21, p < 0.01). The Diptera (excluding the Syrphidae) showed pair-wise associations, rather than associations with site history, and both Arne Old, Arne Restored, Morden Old and Morden Restored were negatively associated with Diptera, while positive associations were found on Hyde old and Hyde Restored. Moreover, the species list in appendix C3 provides circumstantial evidence for a pair-wise association in individual species, such as the digger wasp *Andrena fuscipes* Kirby, the weevil *Apion ulicis* Forster, the bumblebee *Bombus lapidarius* L. and the red wood ant, *Formica rufa* L. On all heathlands, both or one of the bee species, *Apis mellifera* L. and *Bombus lucorum/terrestris*, dominated the visitor

community. There was evidence of a negative association between honeybees and bumblebees on five of the heathlands: honeybee abundance was positively associated with Arne Old, Arne Restored and Holton Restored, while bumblebee abundance was negatively associated with these heathlands (χ^2 = 391.27, d.f. = 7, $p < 0.01$); bumblebees were positively associated with Gore Old and Hyde Old, while honeybees were negatively associated with these old heathlands. The remaining three heathlands showed no evidence of a similar relationship.

Table 3.4 shows the insect-plant ratios for the visitation webs. These ratios were higher for the old heathland in a given pair, although the statistical significance of this was lost when only the core plant species and their interactions were considered, because the pattern was reversed in one pair (full species web: two-sample t = 2.92, p = 0.031; core species web: two-sample t = 2.12, p = 0.062). Patterns were stronger when considering trophic insect species (full species web: two-sample t = 5.51, p = 0.006; core species web: two-sample t = 4.01, p = 0.013). Because of the high number of rare species, the proportion of apparently specialized insect species were high on both old and restored heathlands and in both the full species webs and the core plant species webs.

Generalization is shown in Table 3.5. The mean and median numbers of insect species per plant species were significantly higher on old heathlands than they were on restored heathlands (means: two-sample t = 2.48, p = 0.045; medians: two-sample t = 3.05, p = 0.028). However, the significance of this was lost when considering only insect species, which were present with more than a single specimen per heathland, although in three of the four pairs, the old heathland had the higher value. There were no significant differences among the sites in terms of the number of plant species per insect species.

Table 3.6 shows how the heathlands compared in their redundancy of visitor species. Old heathlands were always similar to each other, but there were no consistent trends for the restored heaths.

3.34 Plant–insect interactions

The number of plant-insect interactions was always higher for the old heathland within a pair (two-sample t = 6.37, p = 0.004), although considerable variation existed among pairs (Table 3.2). As there were no consistent trends for the Shannon-Weaver diversity measures and evenness, the differences among old and restored heathlands were qualitative rather than quantitative. Linkage density and realistic connectance were always higher for the old

heathland within a pair (linkage density: two-sample t = 4.55, p = 0.010; realistic connectance: two-sample t = 5.06, p = 0.007) (Table 3.7). When considering only the core plant species and their interactions, the pattern was unchanged for linkage density, but was lost for realistic connectance (linkage density: two-sample t = 2.7, p = 0.037; realistic connectance: two-sample t = 1.12, p = 0.170). This appears to confirm the sensitivity of C_r to added plant species, which make the restored heathlands appear more different from old heathlands than they perhaps are. However, when grouping taxonomic species into trophic species based on shared interactions, C_r and C_d correlated very strongly (Spearman's Rho = 0.95, p < 0.001) and were always higher for the old heathlands, both within and between pairs (realistic connectance: two-sample t = 4.65, p = 0.009; directed connectance: two-sample t = 3.87, p = 0.015). This was the same for linkage density (two-sample t = 4.04, p = 0.014).

3.35 Visitation patterns

Table 3.8 shows the results of the Mantel tests on the visitation data. In this table listed values are correlation coefficients for two dissimilarity half-matrices and indicate that two webs show similar visitation patterns. However, there were no clear trends in the visitation patterns among the 8 heathlands. Paired sites never showed similar patterns of visitation, and only one restored heath, Hyde Restored, showed similarity to old heathlands (Gore Old and Morden Old). Among the restored heaths, Arne Restored and Morden Restored showed similar patterns, as did Hyde Restored and Holton Restored. Among the old heathlands, similar patterns were found for Arne Old and Hyde Old, Hyde Old and Gore Old and for Gore Old and Morden Old.

3.36 STUDY 2: *quantitative pollen transport data*

A high number (845,845) of pollen grains were sampled, counted and identified overall. A further 269,347 pollen grains were estimated for the total of 493 individual *Apis mellifera* and 158 individual *Bombus lucorum/terrestris*, who visited the same flower species on the same day and in the same transect as 8 conspecifics, whose pollen loads were examined. Seventeen percent of the insect specimens did not carry pollen from the plant species which they were caught on. The number of interaction types, defined as the number of realized plant-insect interactions in each pollen transport web, was similar to the visitation data and

always higher for the old heathland within pairs (two-sample t = 4.41, p = 0.011) (Table 3.9). The 8 quantitative pollen transport webs are shown pair-wise in Figure 3.9 – Figure 3.12. As before, these webs have been drawn to the same scale to provide comparable overviews of the data. In the webs, pollen carried by bees is shown in black and it is immediately evident that this group of insects was the chief pollen carrier. In all but one pair (Morden Old and Morden Restored), more pollen was transported on the old heathland than on the restored heath.

3.37 Specialist pollen carriers and redundancy

Table 3.10 shows the fractions of specialist pollen carrier species in both the full species webs and the core plant species webs. There were no consistent differences among the heathlands and when only the core pollen species were considered, values were similar for 6 of the 8 heathlands. In contrast, the degree of generalization did vary among the heathlands (Table 3.11) and this pattern was evident in both the full species webs and webs from where insect species recorded with only a single specimen had been excluded. In three of the four pairs, both the plant and the insect species were more generalized on the old heathland. In the fourth pair, Hyde Old and Hyde Restored, both the old and restored heath had highly generalized species. Moreover, the old heathlands had a higher degree of redundancy than the restored heaths in three of the four pairs (Table 3.12), while the fourth pair again consisted of Hyde Old and Hyde Restored, which were similar. Furthermore, while the old heathlands were always similar to each other, restored heathlands could be different from other restored heaths as well.

3.38 Pollen–insect interactions

The diversity of pollen carrier interactions was similar both within and between pairs, albeit with varied evenness (Table 3.9). In contrast, quantitative pollen transport interactions were higher for the old heathland in three of the four pairs. Linkage density and connectance were always higher for the old site within all pairs (linkage density: two-sample t = 3.42, p = 0.021; connectance: two-sample t = 4.59, p = 0.010) and were, with one exception, higher for the old heathlands overall (Table 3.13). Including only the core pollen species in the analysis confirmed this pattern (linkage density: two-sample t = 3.07, p = 0.027; connectance: two-sample t = 2.89, p = 0.031). When species were lumped into trophic species, the significance was lost (linkage density: two-sample t = 1.89, p = 0.078; realistic

connectance: two-sample t = 1.33, p = 0.140; directed connectance: two-sample t = 0.76, p = 0.250), although in three pairs of four, values were higher for the old heathland.

3.39 Pollen transport patterns

Apart from Hyde Restored, all heathlands were similar in terms of their pollen carrier patterns, i.e. similar numbers of insect species were found to transport the pollen of the most widespread plant species (Table 3.14). What set Hyde Restored apart from the other heathlands was the low number of shared pollen carriers between *Calluna vulgaris* and both of *Erica cinerea* and *Ulex minor* on this site. However, the picture was slightly different for the quantitative pollen transport patterns (Table 3.15). Among the old and restored heathlands, only Holton Restored was significantly similar to the four old sites. Hyde Restored was similar only to Arne Old, and Morden Restored was similar only to Hyde Old. Only two restored sites, Holton Restored and Morden Restored were significantly similar to each other. In contrast, apart from Arne Old and Gore Old, all old sites were similar to each other. Hyde Restored was no longer set apart from the other heathlands.

3.4 DISCUSSION

In this section, I first review the evidence for each of the four models and evaluate the success of the heathland restoration schemes. I then go on to discuss the possible causes of observed patterns, both with respect to the insect and plant communities. Finally, I discuss the limitations of the study.

3.41 Model summary

Model 1: *were restored heathlands similar to adjacent old heathland?* In terms of insect species, restored heaths were most diverse where they were paired with a species-rich old heathland. However, restored heaths did not share more species with their paired sites than they did with other sites. So although the species richness on restored heaths correlated with that of adjacent heathland, it was not caused by it. Hence there was no evidence of a shared similarity caused by the migration of species from adjacent heathland onto restored sites.

Model 2: *were restored heathlands similar to other restored heathlands?* Restored heathlands were similar in terms of plant species richness and the abundance of flowers and insects. In functional terms, restored heaths were also simpler than old heathlands and had lower values of linkage density and connectance in both the full visitation data and the full pollen transport data and they were less generalized.

Model 3: *were restored heathlands similar to both old and restored heathlands?* The diversity of the insect communities and the number of shared insect species were similar across all heathlands. Moreover, the two bee species, *Apis mellifera* and *Bombus lucorum/terrestris*, were dominant on all sites. Likewise, fractions of specialist insect species were similar on old and restored heathlands. With respect to function, there was a comparable diversity of interaction types across all heaths and plants enjoyed similar patterns of pollen carriers. Trimming the webs to only the core plant species and their interactions resulted in very similar web statistics, and as these plant species were the most abundant, differences in web statistics among the heathlands were qualitative rather than quantitative.

Model 4: *were there no consistent trends in the similarity of restored heathlands to other heathlands?* Although old heathlands were similar to each other, restored sites showed no consistent trends with respect to visitation and quantitative pollen transport patterns, or in

insect redundancy. Only few combinations involving restored sites were significant, and these showed no sign of being related to pairs or to site history.

Although evidence was found for all four models, most of it supported Model 2 and Model 3. The lower abundance of flowers and insects on restored heathlands is likely to be directly related with their young age. Therefore, Model 3 will increasingly stand out as more applicable over time.

3.42 The outcome of the restoration schemes

Although the old heathland in a pair was always richer in insect species than the restored heath, all the heathlands shared some fundamental food web structures. Furthermore, the restored heaths all had a very comparable diversity of core plant species to that of old heathlands. When non-core plant species were removed from the data, patterns disappeared whereby the restored sites had initially appeared distinct. These additional plant species may be regarded as noise in the data, because they were very rare relative to the core species and would be expected to disappear as the vegetation matures on the restored heathlands. There was some evidence of biodiversity being related to locality but although paired sites would correlate in species richness, they did not have more species in common than they did with other heathlands.

Although directed connectance was higher on old heathlands, there was no sign of visitation patterns being related to either site history or locality. However, in contrast to restored sites, old heathlands had both similar pollen carrier and quantitative pollen transport patterns. Therefore insects behaved differently among the old and restored heathlands.

Heathland restoration should be regarded as a process of returning communities to within the boundaries of natural variation (White and Walker 1997). After ten years, the restored heathlands have reached this state with regard to visitation patterns, but not with regard to quantitative pollen transport patterns. However, since the pollen carrier patterns were similar among the majority of old and restored heathlands, the restoration of quantitative pollen transport is expected to follow as the vegetation matures. That restored heathlands are still changing may be indicated by their lower values of linkage density. Although more plant species were found on restored heathlands, the overall flower abundance was dominated by fewer species than was the case on old heathlands. Therefore, interactions were more likely to be with fewer plant species. Pimm *et al.* (1991) found that

food webs with low values of linkage density were more likely to be invaded. In their models, an increase in one prey species could cause an increase in a shared predator and therefore indirectly bring about a decline in other prey species. However, plant-pollinator webs describe mutualisms rather than predation, and we sometimes consider abundant flower species to be community keystones that attract pollinators into the system to the benefit of other plant species (e.g. Memmott 1999). Nevertheless, when the flowers of one plant species vastly outnumber the flowers of other plant species, insects may choose not to forage on the rare species. The question is whether this is a problem on restored heathlands? Since most heathland plants are perennials, pollinator competition is unlikely to be as critical as in systems with many annual plant species, such as hay meadows. As the heathlands mature, the number of heathland plant species increases and their relative abundance becomes more even (Marrs and Lowday 1992). Here the 10-year-old restored heathlands already contained most of the heathland plants. Therefore, as the vegetation matures, insects will find it increasingly worthwhile foraging on other flower species.

3.43 The diversity of insect visitors

Because restored heaths did not share more species with adjacent old heathland than with heathlands elsewhere, the colonisation ability of insect species may be greater than assumed in Model 1, such that, in effect, all the study sites are adjacent to each other. However, individual species of insect vary hugely in their migratory ability. For example, Thomas and Harrison (1992) observed a high degree of patch loyalty in populations of the silver-studded butterfly, *Plebejus argus* L., and colonisation into suitable habitat more than 1 kilometre away from source populations was extremely rare. In contrast, the heathland sampling revealed species of hoverfly, *Episyrphus balteatus* DeGeer, *Metasyrphus corollae* Fabricius and *Sphaerophoria scripta* L. that are known to occasionally migrate from mainland Europe (Stubbs 1983), and a butterfly, *Cynthia cardui* L., which migrates from north Africa (Higgins 1983). An underlying rationale in restoring heathland near extant heath is that species colonisation will be greatly aided by the short distance. However, only the non-syrphid flies were associated with pair in the present study, although there was circumstantial evidence for a pair-wise association in some individual species.

Perhaps more importantly, the study found many examples of species which are common in other habitats than heathland. These include the hoverflies *Episyrphe*

grossulariae Meigen, *Episyrphus balteatus*, *Metasyrphus luniger* Meigen and the bumblebees, *Bombus pascuorum* Scopoli and *Bombus terrestris/lucorum* that are also found in arable situations and urban gardens (Stubbs 1983; Benton 2000). Therefore the surrounding habitat matrix might be responsible for many of the species which were recorded on the heathlands, and the reason why biodiversity was associated with locality. In a study of the Coleoptera, Hemiptera and Araneae on fragmented Dorset heathlands, Webb and Hopkins (1984) found an increased species diversity on the most fragmented sites and attributed this to edge effects, with many vagrant insect species originating in species-rich surrounding habitat. Thus, although biodiversity measures can be useful indicators of ecosystem stability (Tilman and Downing 1994; Kareiva 1996; Kwak *et al.* 1996), they are not necessarily useful when evaluating the success of heathland restoration schemes, because the heathlands often have fewer species than the surrounding habitat matrix (Webb and Hopkins 1984).

The old heathlands had more insect species and a higher degree of redundancy than the restored heaths. Lawton (1994) hypothesized that numerous rare species which are apparently redundant under benign conditions, may provide 'backup systems' for ecological processes under extreme events, as suggested by studies linking biodiversity and ecosystem function (Naeem *et al.* 1994; Tilman and Downing 1994; Tilman *et al.* 1996). However, the extrapolation from controlled and simple systems, such as the Ecotron (Lawton 1994) or plots of grassland that vary in degree of species poverty (Tilman and Downing 1994), is problematic, especially in situations like the present where the surrounding matrix may be more species rich that the heathlands. Lawton (1994) termed it 'foolish' and called for more data from natural, semi-natural and artificial ecosystems. Although the present data suggest that redundancy in the pollinator community may be higher on old than on restored heathlands, they do not reveal if the difference is great enough for redundancy to have a measurable impact. For example, Morden Old had only four more insect species than Morden Restored. It seems unlikely that this slight difference would make the old heathland quantifiably better buffered against adversity. It would be interesting to monitor the pollination on these heathlands over several years to include both 'good' and 'poor' seasons that would reveal if old and restored heathlands do indeed respond differently to changes in conditions.

While the plant community was generalized, the pollinator community appeared to be less so. However, many insect species were present at low density and therefore these

species could be more generalized than revealed here. Naturally, when species recorded with only a single specimen were excluded from the analysis, this always increased the generalization ratios. However, future work could consider a more selective sampling, whereby the rare species were sampled more intensively in order for their feeding habits and pollen loads to be better replicated.

Heathland specialists occurred on both old and restored heathlands. For example, the solitary bees *Andrena fuscipes* and *Colletes succinctus* L. that are strongly associated with *Calluna* (Proctor and Yeo 1973; Betts and Laffoley 1986) occurred on most sites although never at high densities. In contrast, *Andrena ovatula* Kirby, *Lasioglossum lativentre* Schenk and *Lasioglossum prasinum* Smith were found only on old heathlands, but likewise not at high densities. Therefore, it could be hypothesized that these heathland species are not of particular importance in the pollination of heathland plants. However, rare pollinators can be very important. For example, Dicks (2002) found that rare pollinators were efficient pollinators of ox-eye daisy, *Chrysanthemum leucanthemum* L., and it is possible that solitary bees are equally efficient pollinators of some heathland plants, such as *Ulex minor*. These bees appeared more specialized, especially to *U. minor*, than other bees. When insects and plants interact more strongly with each other than they do with other species in the webs, they are said to form a compartment (Raffaelli and Hall 1992; Corbet 2000; Dicks *et al.* 2002). Hence the potential presence of compartments can be very relevant when attempting to restore the webs, because adequate pollination may not occur if compartments are not reinstated. As a consequence, Chapter 4 will deal with heathland compartments in detail.

Some flower-visiting species are effectively heathland specialists because they prey upon obligate flower visitors and require loose soil for their nests. One example is the European beewolf, *Philanthus triangulum* Fabricius, which preys mainly upon *Apis mellifera* (Strohm and Linsenmair 1998). This wasp catches a honeybee on a flower, paralyses it and takes it to an underground nest cell where 3-6 honeybees will provide enough food for one *P. triangulum* larva. An adult wasp can catch about 100 bees in its lifetime but because honeybees are so common on the heathlands, this is unlikely to have any measurable effect on the pollinator community of the three sites where the species occurred.

The beewolf example illustrates that not all insects in the study visit flowers to feed on pollen or nectar, even though they can carry pollen and effect some pollination. To these

insects, floral composition is indirectly important because their prey depend on it. In other cases, floral visitors may not have been feeding at all, but merely used the flower heads as convenient places to display themselves, although at other times they could be feeding on floral rewards. In contrast, the damselfly, *Enallagma cyathigerum* Charpentier, which was found at Morden Restored, does not feed in its adult stage, and must exclusively have used the flower head as a sunning spot.

Other species are associated with the grazing management on the heathlands. These include the cluster flies, *Pollenia* spp., and the dung fly, *Scathophaga stercoraria* L., that lay their eggs on dung, as well as the autumn fly, *Musca autumnalis* DeGeer, whose adults feed on the mucous secretions from the eyes and noses of cattle and horses. However, these species also feed on floral rewards and carry pollen.

3.44 The importance of the floral composition

Because the seed bank of *Calluna vulgaris* is more abundant and long lived than that of *Erica cinerea* (Bakker *et al.* 1996, but see Thomson and Band 1997), *Calluna* is normally much more abundant on young heathlands than on old dry lowland heaths, where *E. cinerea* is co-dominant. *Calluna* begins flowering later than *E. cinerea* and this means that fewer floral resources are available on restored sites in early summer. Many species of both Hymenoptera and Syrphidae were found to feed on this plant. As the restored heathlands mature, *E. cinerea* is expected to become more abundant, and the overall floral constancy expected to become more similar to that of old heathlands. As a consequence, a higher abundance and diversity of insects may result. Meanwhile, the delayed flowering on restored heaths can act as an invasion filter, screening out the spring-active insects and preventing them from establishing. The species which are already present feed mainly on *Calluna* because this is by far the most abundant flower species. It is perhaps a consequence of the floral composition that restored heathlands do not show similar quantitative pollen transport patterns.

3.45 Temporal data

An obvious limitation to the current study is the lack of temporal replication – the data are from one year only. Insect populations often fluctuate from year to year, in response to variations in the weather, disturbance regimes, predation, overwintering success, competition, etc. Gilbert and Owen (1990) showed how hoverfly populations in an English

suburban garden varied markedly over a 15-year-period, and they concluded that at least some hoverfly communities are merely 'coincidences of species in space and time', with evidence neither of species competition nor of emergent community properties. Because the present study compares sites within the same year, it has been assumed that these sites exhibit a similar pattern of variation, in response to the same weather conditions across the eight heathlands. However, this assumption should be tested. For example, it is possible that the insect community on a site with a diverse topography and range of surrounding habitat is more resilient to extreme events compared to communities on more uniform sites, not because of redundancy but because of habitat quality.

3.46 Other limitations

The present study was biased towards day-flying insects. However, night sampling would pose a problem in regards to quantitative visitation sampling, because the use of torches might change the behaviour of night-active insects. Ideally though, future studies should include pollen quantitative pollen transport data for nocturnal insects.

Another limitation was the bias towards big insects. For example, flower thrips (Thysanoptera) are very small insects that live most of their lives on or inside flowers. They are found in the flowers of *Calluna vulgaris*, *Erica cinerea* and *Erica tetralix* and, though they feed on the pollen and flower tissue, thrips have been demonstrated to effect pollination in *Calluna* and *E. tetralix* (Hagerup 1950; Hagerup and Hagerup 1953). Chapter 6 deals with thrips in detail.

Finally, a greater degree of replication might have been desirable. Having only four heathland pairs posed limitations to the statistical analysis possible to compare these sites. However, using a paired design was an efficient way to account for some of the variation. This is illustrated in Figure 3.7. Although considerable variation existed among pairs, distinct trends existed within pairs. Moreover, additional restored sites could not be located that were comparable to the four restored heaths in terms of location, age and site history. Finally, since heathland sampling and laboratory analysis both proved very time consuming, an increased level of replication could have resulted in less well-resolved webs. While this may be permissible in future studies, a high sampling effort, as provided with the present data, is needed to identify the curve of diminishing information with increased sampling effort.

TABLES

Table 3.1 Four pairs of dry lowland heathland in the Poole Basin, Dorset. Old = ancient heathland, Restored = heathland restored in the early 1990s. Listed sizes are approximate estimates of the open heathland on which sampling plots were established. Typically, the sites formed part of a heathland matrix. Hence the size of an individual site is not a measure of the total heathland area at each locality.

Pair	Study site	Locality	Grid reference	Size (ha)
1	Arne Old	Grip Heath	SY 976 875	30
	Arne Restored	Grip Heath	SY 976 878	8
2	Gore Old	Great Ovens	SY 926 902	25
	Holton Restored	Holton Lee	SY 957 919	15
3	Hyde Old	Lower Hyde	SY 886 911	18
	Hyde Restored	Lower Hyde	SY 878 908	2
4	Morden Old	Morden Bog	SY 915 922	16
	Morden Restored	Morden Bog	SY 911 923	8

Table 3.2 Basic web statistics, insect sample sizes (N) and Shannon-Weaver indices (*H'*) and evenness (E) for both the insect communities and the interaction (Int.) types. Interaction types are defined as the number of realized plant-insect interactions in each web. The table includes only transect plant species, although web diagrams may show plant species found *in situ* but not in transects, similar to the style in Dicks *et al.* (2002).

	Plant species	Insect species	N	Int. types	Insect H'	Insect E	Int. H'	Int. E
Arne Old	5	34	463	48	1.53	0.43	2.20	0.57
Arne Restored	8	23	212	33	1.49	0.48	2.06	0.59
Gore Old	7	43	367	73	2.44	0.65	3.38	0.79
Holton Restored	8	38	352	51	1.65	0.45	2.31	0.59
Hyde Old	6	48	422	74	2.56	0.66	3.27	0.76
Hyde Restored	10	41	205	63	2.86	0.77	3.53	0.85
Morden Old	6	32	351	51	1.76	0.51	2.65	0.67
Morden Restored	6	28	351	38	1.52	0.46	2.34	0.64

Table 3.3 Shared insect species, expressed as the proportion of the insect species found on the heathland listed to the left of the table.

	Arne Old	Arne Restored	Gore Old	Holton Restored	Hyde Old	Hyde Restored	Morden Old	Morden Restored
Arne Old	-	0.34	0.59	0.47	0.47	0.47	0.47	0.34
Arne Restored	0.52	-	0.65	0.57	0.57	0.65	0.52	0.48
Gore Old	0.47	0.35	-	0.47	0.60	0.51	0.51	0.37
Holton Restored	0.42	0.34	0.53	-	0.53	0.58	0.45	0.37
Hyde Old	0.33	0.27	0.54	0.42	-	0.54	0.42	0.35
Hyde Restored	0.39	0.37	0.54	0.54	0.63	-	0.46	0.34
Morden Old	0.50	0.38	0.69	0.53	0.63	0.59	-	0.47
Morden Restored	0.43	0.39	0.57	0.50	0.61	0.57	0.54	-

Table 3.4 Insect-plant ratios and specialist ratios for the full and core species visitation webs, respectively.

	Full species webs			Core species webs		
	Insect species / plant species	Trophic insect species / plant species	Specialist insect species / all insect species	Insect species / plant species	Trophic insect species / plant species	Specialist insect species / all insect species
Arne Old	6.80	2.00	0.74	6.80	2.00	0.74
Arne Restored	2.88	0.50	0.61	4.60	0.80	0.61
Gore Old	6.14	2.14	0.72	7.17	2.50	0.72
Holton Restored	4.75	1.25	0.79	6.00	1.50	0.78
Hyde Old	8.00	1.83	0.69	10.75	2.25	0.65
Hyde Restored	4.10	1.20	0.66	8.00	2.00	0.65
Morden Old	5.33	2.00	0.63	6.40	2.40	0.63
Morden Restored	4.67	1.00	0.71	6.75	1.25	0.70

Table 3.5 The mean and median numbers of insect species per plant species and plant species per insect species in the visitation webs. Values are given for both the full species webs, as well as for webs excluding species recorded with only one specimen on each heathland.

	Full species webs				Webs excluding single-specimen species			
	Insects / plant sp.		Plants / insect sp.		Insects / plant sp.		Plants / insect sp.	
	Mean	Median	Mean	Median	Mean	Median	Mean	Median
Arne Old	9.60	7.00	1.41	1.00	5.60	4.00	1.93	2.00
Arne Restored	8.25	6.00	1.43	1.00	5.75	5.50	1.77	2.00
Gore Old	12.17	11.00	1.74	1.00	10.60	10.00	2.41	2.00
Holton Restored	8.50	5.50	1.34	1.00	4.50	3.50	1.87	2.00
Hyde Old	14.80	8.00	1.54	1.00	10.60	8.00	1.96	2.00
Hyde Restored	9.00	6.00	1.54	1.00	7.00	6.00	2.00	2.00
Morden Old	10.20	11.00	1.59	1.00	8.25	9.50	2.36	2.00
Morden Restored	9.50	6.00	1.36	1.00	7.67	8.00	1.77	2.00

Table 3.6 Comparisons of visitation web redundancy. Read horizontally, listed values are significant t statistics from paired t tests on whether the numbers of insect species per plant species on the heathland at the left side of the table are higher than those of the same plant species on other heathlands. * $p<0.05$, ** $p<0.025$, *** $p<0.01$.

	Arne Old	Arne Restored	Gore Old	Holton Restored	Hyde Old	Hyde Restored	Morden Old	Morden Restored
Arne Old	-	2.30*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Arne Restored	n.s.	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Gore Old	n.s.	3.45*	-	n.s.	n.s.	n.s.	n.s.	n.s.
Holton Restored	n.s.	4.74***	n.s.	-	n.s.	n.s.	n.s.	2.45*
Hyde Old	n.s.	3.18**	n.s.	2.71*	-	n.s.	n.s.	4.11**
Hyde Restored	n.s.	3.80***	n.s.	n.s.	n.s.	-	n.s.	2.49*
Morden Old	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-	n.s.
Morden Restored	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-

Table 3.7 Linkage density (L), relative connectance (C_r) and, where applicable, directed connectance (C_d) for the full taxonomic visitation webs, the core species webs and the trophic species webs, respectively.

	Full species webs		Core species webs		Trophic species webs		
	L	C_r	L	C_r	L	C_r	C_d
Arne Old	1.23	0.28	1.23	0.28	1.33	0.40	0.09
Arne Restored	1.06	0.18	1.18	0.29	0.58	0.22	0.05
Gore Old	1.46	0.24	1.49	0.29	1.68	0.35	0.08
Holton Restored	1.11	0.17	1.17	0.23	1.11	0.25	0.06
Hyde Old	1.37	0.26	1.45	0.40	1.35	0.35	0.08
Hyde Restored	1.24	0.15	1.36	0.31	1.18	0.22	0.05
Morden Old	1.34	0.27	1.38	0.32	1.22	0.31	0.07
Morden Restored	1.12	0.23	1.19	0.34	0.75	0.25	0.06

Table 3.8 Significant correlation coefficients from Mantel analyses on the similarity of flower visitation patterns. * $p<0.05$, ** $p<0.025$, *** $p<0.01$, **** $p<0.0005$.

	Arne Old	Arne Restored	Gore Old	Holton Restored	Hyde Old	Hyde Restored	Morden Old
Arne Restored	n.s.						
Gore Old	n.s.	n.s.					
Holton Restored	n.s.	n.s.	n.s.				
Hyde Old	0.76*	n.s.	0.82*	n.s.			
Hyde Restored	n.s.	n.s.	0.95***	0.98****	n.s.		
Morden Old	n.s.	n.s.	0.86*	n.s.	n.s.	0.72*	
Morden Restored	n.s.	0.77**	n.s.	n.s.	n.s.	n.s.	n.s.

Table 3.9 The number of interaction types, defined as the number of realized plant-insect interactions in each pollen transport web, and Shannon-Weaver indices (*H'*) and evenness (E) for both the pollen carrier and the quantitative pollen transport interactions. All interactions with pollen species not growing in transects or interactions involving less than 5 grains have been excluded.

	Int. types	Pollen carrier int. H'	Pollen carrier int. E	Quantitative int. H'	Quantitative int. E
Arne Old	55	2.12	0.53	2.06	0.51
Arne Restored	32	2.12	0.61	1.60	0.46
Gore Old	71	3.41	0.80	2.71	0.64
Holton Restored	52	2.63	0.67	1.65	0.42
Hyde Old	65	3.18	0.76	2.03	0.49
Hyde Restored	59	3.67	0.90	2.45	0.60
Morden Old	57	2.72	0.67	2.29	0.57
Morden Restored	41	2.55	0.69	1.56	0.42

Table 3.10 Specialist ratios for the full species and core species pollen transport webs, respectively.

	Full species webs	Core species webs
	Specialist insect species / all insect species	Specialist insect species / all insect species
Arne Old	0.43	0.43
Arne Restored	0.58	0.58
Gore Old	0.55	0.58
Holton Restored	0.57	0.58
Hyde Old	0.56	0.59
Hyde Restored	0.40	0.53
Morden Old	0.35	0.38
Morden Restored	0.36	0.41

Table 3.11 The mean and median numbers of insect species per pollen species and pollen species per insect species in the pollen transport webs. Values are given for both the full species webs, as well as for webs excluding species recorded with just one specimen.

	Full species webs				Webs excluding single-specimen species			
	Insects / pollen sp.		Pollen / insect sp.		Insects / pollen sp.		Pollen / insect sp.	
	Mean	Median	Mean	Median	Mean	Median	Mean	Median
Arne Old	8.29	6.00	2.07	2.00	5.14	5.00	2.33	2.00
Arne Restored	6.40	3.00	1.68	1.00	4.60	4.50	1.77	1.00
Gore Old	9.38	6.50	2.42	1.00	7.88	6.00	2.86	2.00
Holton Restored	5.70	5.00	2.04	1.00	4.44	3.00	2.60	2.00
Hyde Old	7.27	3.00	2.25	1.00	6.50	6.00	2.52	2.00
Hyde Restored	7.90	7.00	2.63	2.00	6.60	6.50	3.00	3.00
Morden Old	7.88	8.00	2.42	2.00	5.25	5.50	2.93	2.00
Morden Restored	6.57	4.00	2.09	2.00	4.57	3.00	2.46	2.00

Table 3.12 Redundancy in the pollen transport webs. Read horizontally, listed values are significant t statistics from tests on whether the number of pollen-carrier species per plant species on the heathland to the left of the table is higher than those of the other heathlands. * $p<0.05$, ** $p<0.025$, *** $p<0.01$.

	Arne Old	Arne Restored	Gore Old	Holton Restored	Hyde Old	Hyde Restored	Morden Old	Morden Restored
Arne Old	-	8.63***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Arne Restored	n.s.	-	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Gore Old	n.s.	2.71*	-	2.14*	n.s.	n.s.	n.s.	n.s.
Holton Restored	n.s.	3.48***	n.s.	-	n.s.	n.s.	n.s.	3.80***
Hyde Old	n.s.	2.50*	n.s.	n.s.	-	n.s.	n.s.	n.s.
Hyde Restored	n.s.	2.67**	n.s.	n.s.	n.s.	-	n.s.	2.71**
Morden Old	n.s.	3.73***	n.s.	n.s.	n.s.	n.s.	-	3.25**
Morden Restored	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-

Table 3.13 Linkage density (L), relative connectance (C_r) and, where applicable, directed connectance (C_d) for the full taxonomic pollen transport webs, the core species pollen transport webs and the trophic species pollen transport webs, respectively.

	Taxonomic webs		Core species webs		Trophic species webs		
	L	C_r	L	C_r	L	C_r	C_d
Arne Old	1.41	0.32	1.41	0.32	1.68	0.46	0.09
Arne Restored	1.03	0.17	1.03	0.28	1.27	0.47	0.12
Gore Old	1.42	0.24	1.42	0.26	1.79	0.52	0.13
Holton Restored	1.13	0.17	1.13	0.24	1.81	0.48	0.11
Hyde Old	1.20	0.23	1.24	0.39	1.70	0.71	0.17
Hyde Restored	1.16	0.14	1.16	0.30	1.64	0.51	0.12
Morden Old	1.50	0.30	1.50	0.36	2.13	0.62	0.13
Morden Restored	1.21	0.24	1.38	0.33	1.71	0.60	0.12

Table 3.14 Significant correlation coefficients from Mantel analyses on the similarity of pollen carrier patterns. * $p<0.05$, ** $p<0.025$.

	Arne Old	Arne Restored	Gore Old	Holton Restored	Hyde Old	Hyde Restored	Morden Old
Arne Restored	0.97**						
Gore Old	0.85*	0.87*					
Holton Restored	0.97**	0.97**	0.72*				
Hyde Old	0.97**	0.99**	0.92**	0.98**			
Hyde Restored	n.s.	n.s.	n.s.	n.s.	n.s.		
Morden Old	0.94*	0.94*	0.90**	0.98**	0.98**	n.s.	
Morden Restored	0.95**	0.93*	0.79*	0.97**	0.95**	n.s.	0.95**

Table 3.15 Significant correlation coefficients from Mantel analyses on the similarity of quantitative pollen transport patterns. * $p<0.05$, ** $p<0.025$.

	Arne Old	Arne Restored	Gore Old	Holton Restored	Hyde Old	Hyde Restored	Morden Old
Arne Restored	n.s.						
Gore Old	n.s.	n.s.					
Holton Restored	0.81*	n.s.	0.73*				
Hyde Old	0.78*	n.s.	0.82*	0.95**			
Hyde Restored	0.71*	n.s.	n.s.	n.s.	n.s.		
Morden Old	0.65*	n.s.	0.81**	0.88*	0.88**	n.s.	
Morden Restored	n.s.	n.s.	n.s.	0.88*	0.86*	n.s.	n.s.

FIGURES

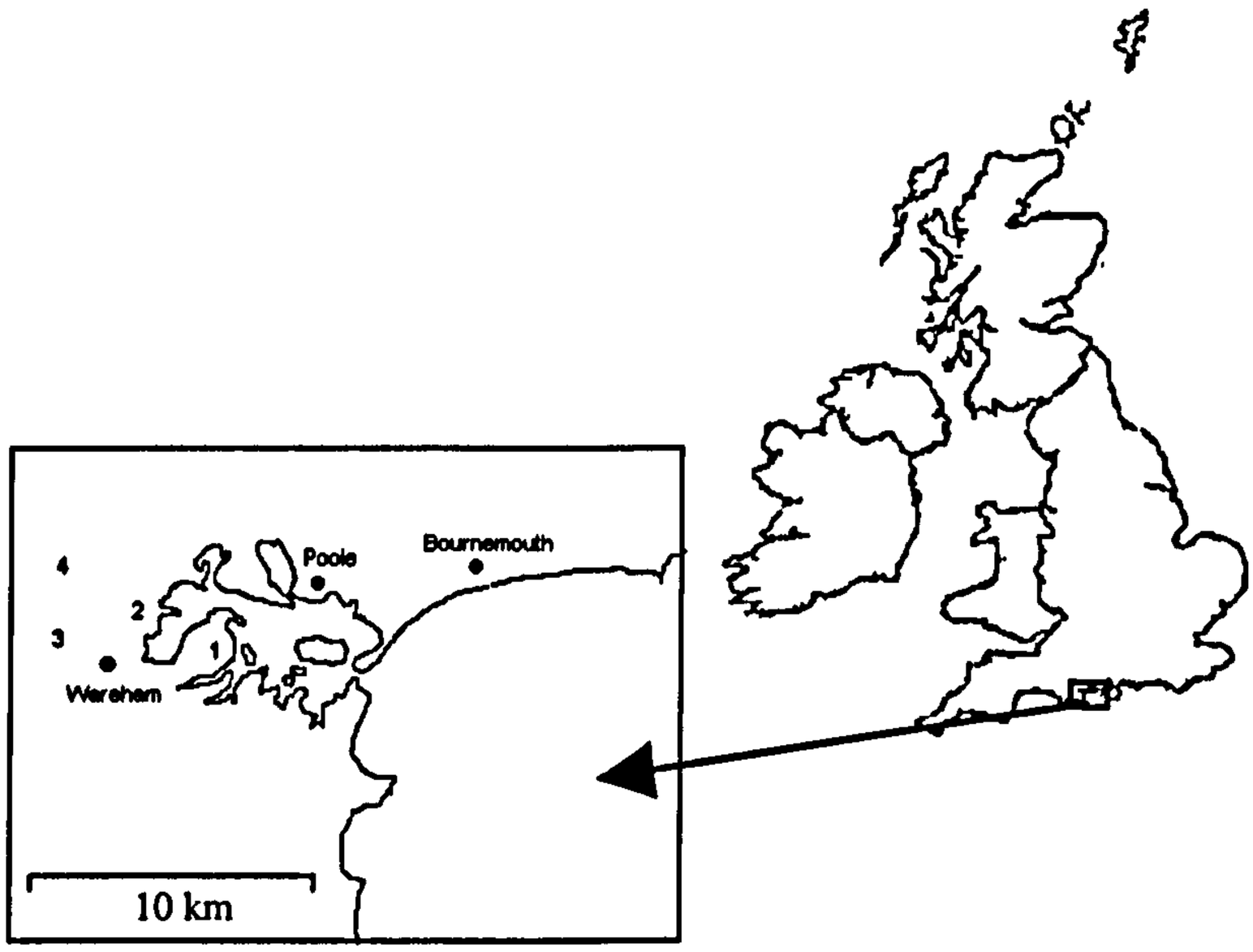


Figure 3.1 A map of Poole Harbour in Dorset, South England, showing the location of the 4 pairs of heathland (see also Table 3.1).

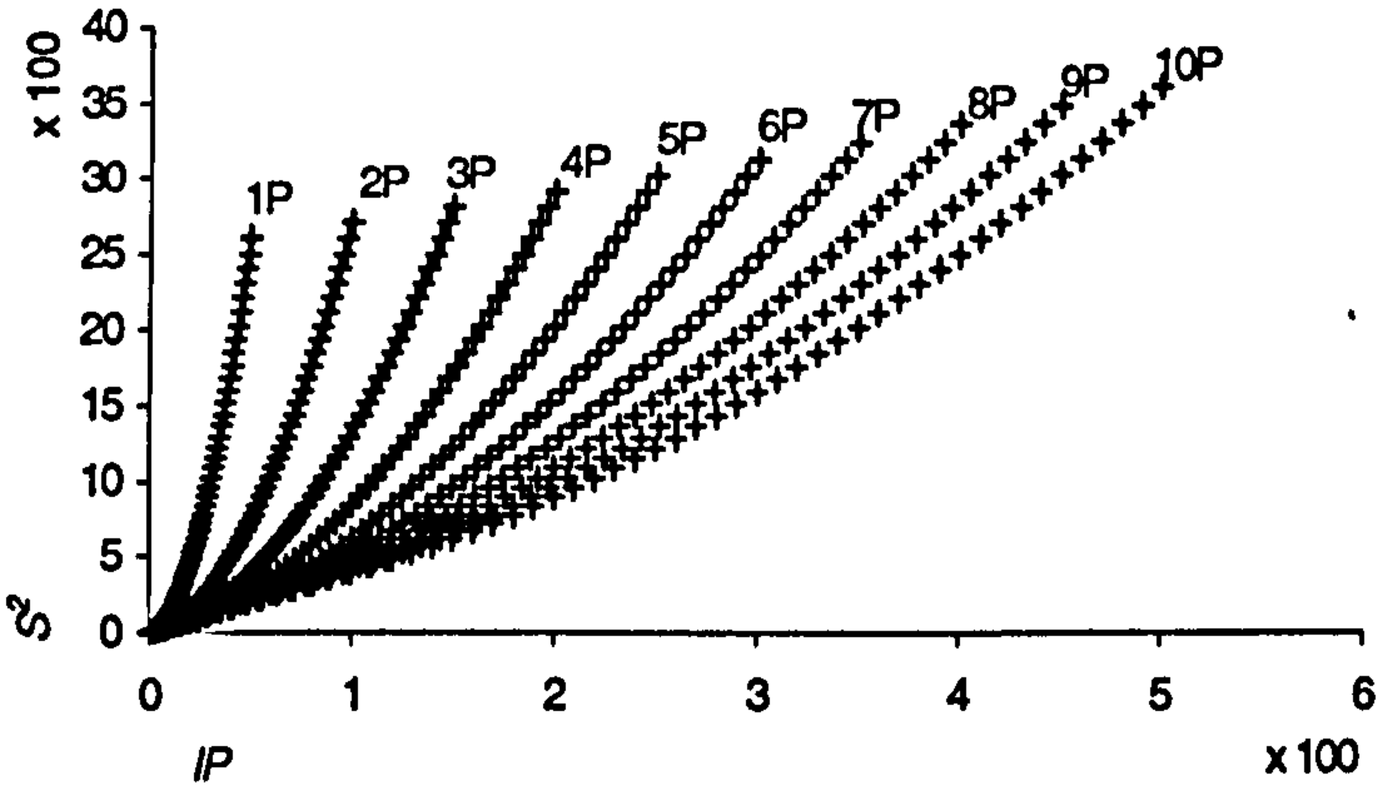
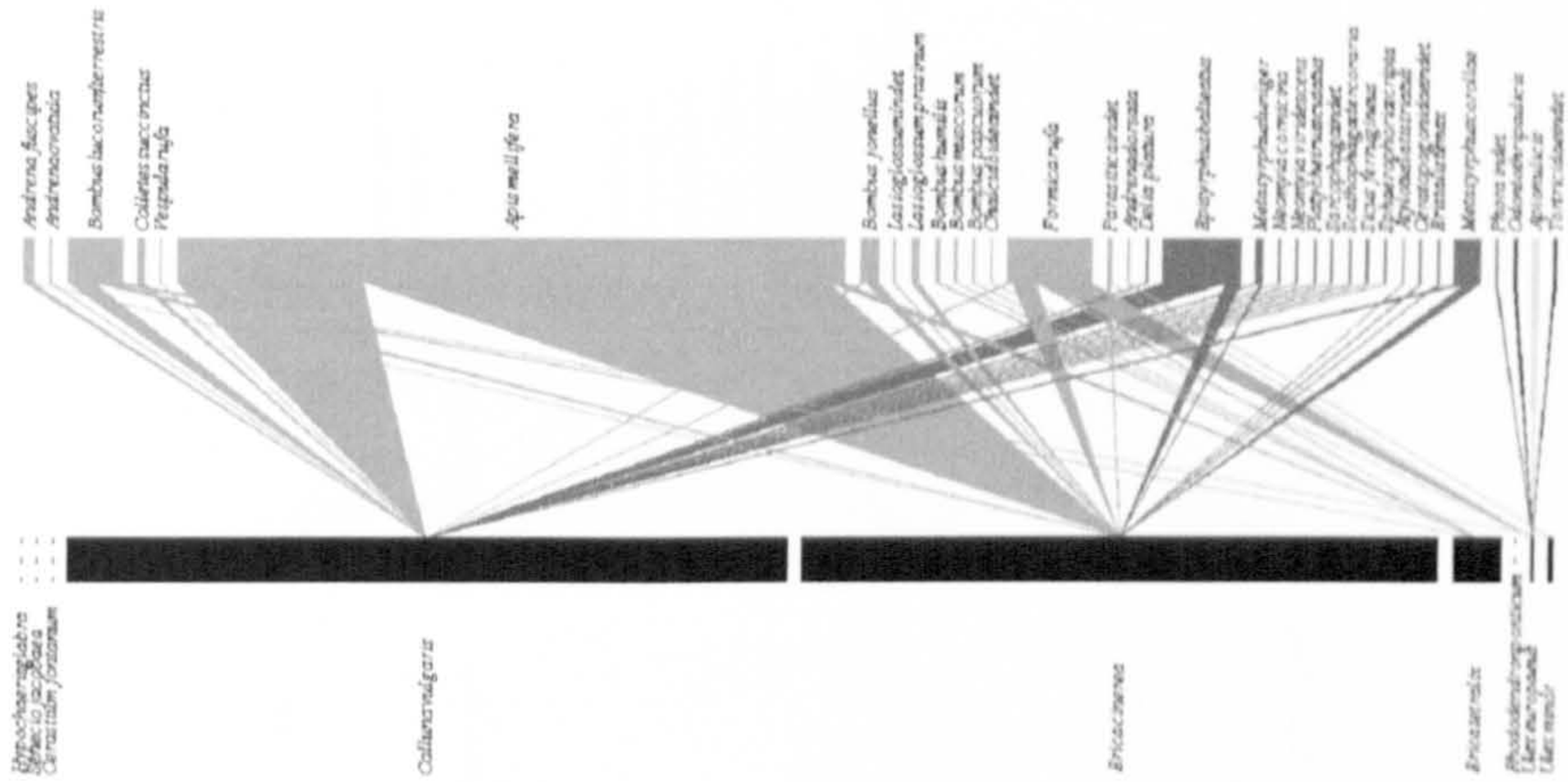


Figure 3.2 The relationship of IP (C_r) and S^2 (C_d) in all possible webs of 1-10 plant species and 1-50 insect species. In webs with increasing insect species/plant species ratios, isobars emerge in the IP distribution that are directly associated with the number of plant species (labelled 1P – 10P) (see text, section 3.25).

(a) Arne Old



(b) Arne Restored

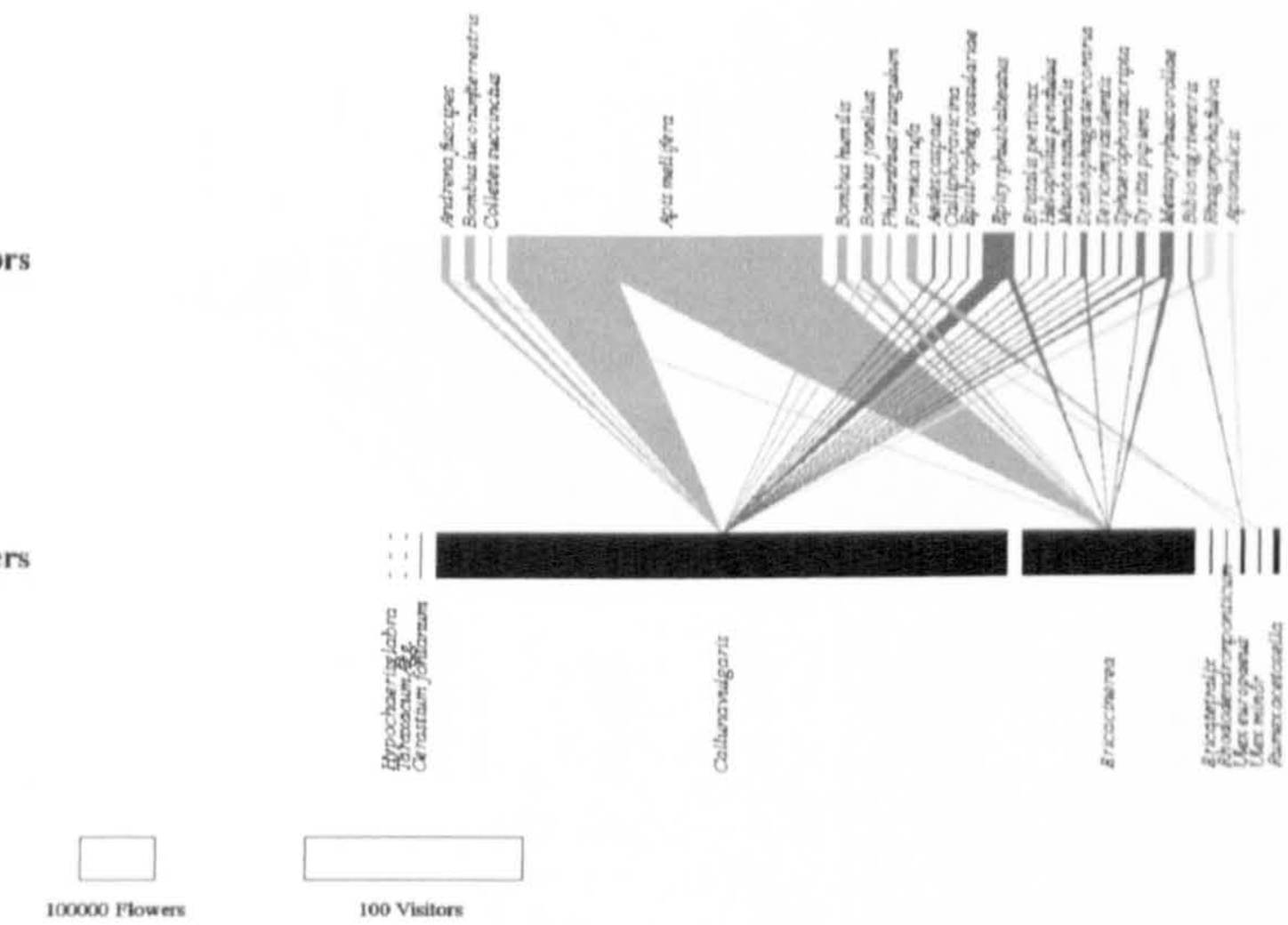
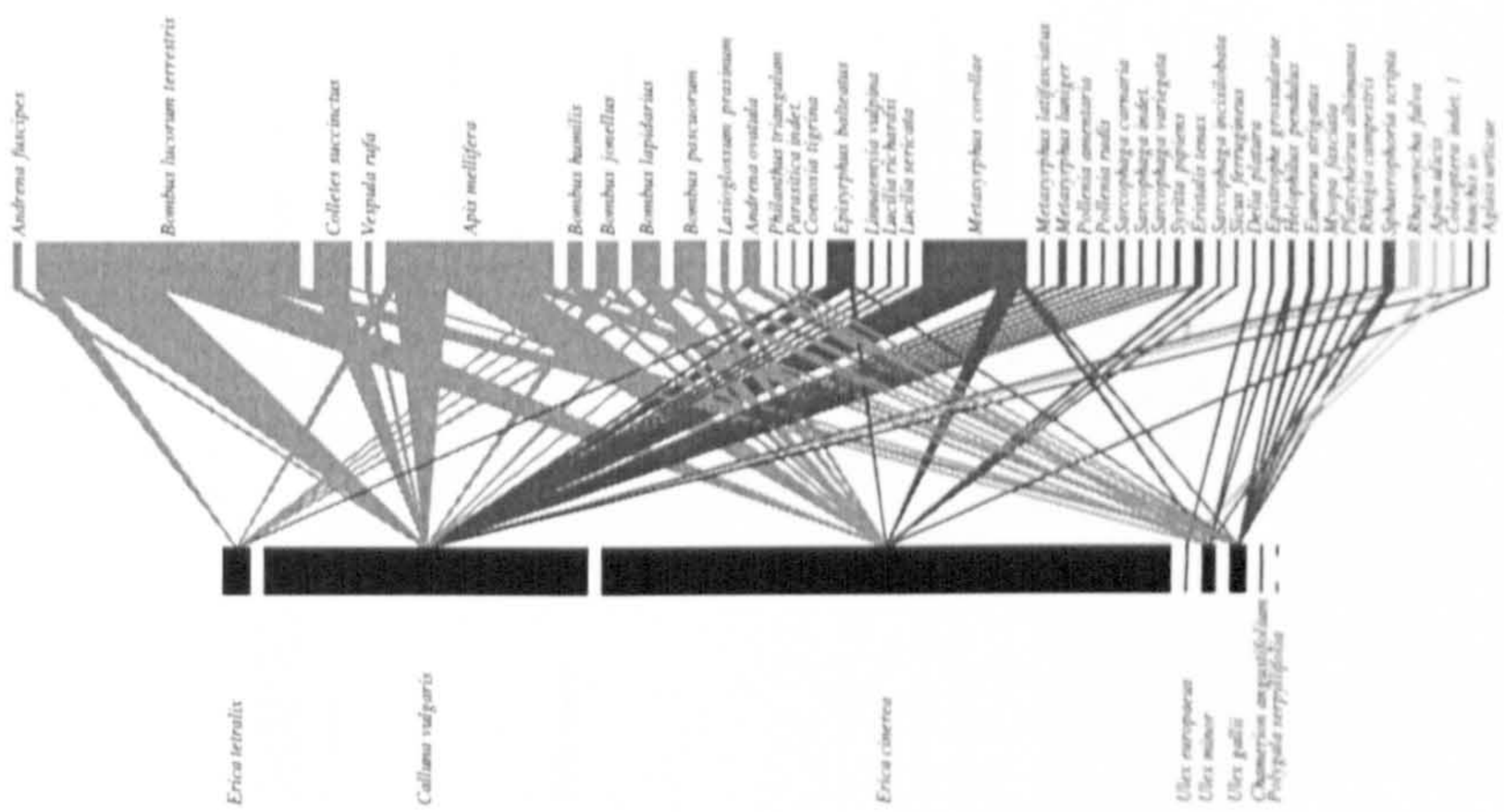


Figure 3.3 Quantitative flower visitation webs for: a) Arne Old and b) Arne Restored. Flower species are shown as rectangles at the bottom of each web, insects are shown above and interactions link plants and insects. The relative abundance of each species is indicated by the width of the rectangles and the frequency of each interaction type is indicated by the width of the line. Flower species shown by a stippled line were present on the heathland but not recorded in transects. The different insect orders are shown in different shades of grey. Webs are drawn to the same scale.

(a) Gore Old



(b) Holton Restored

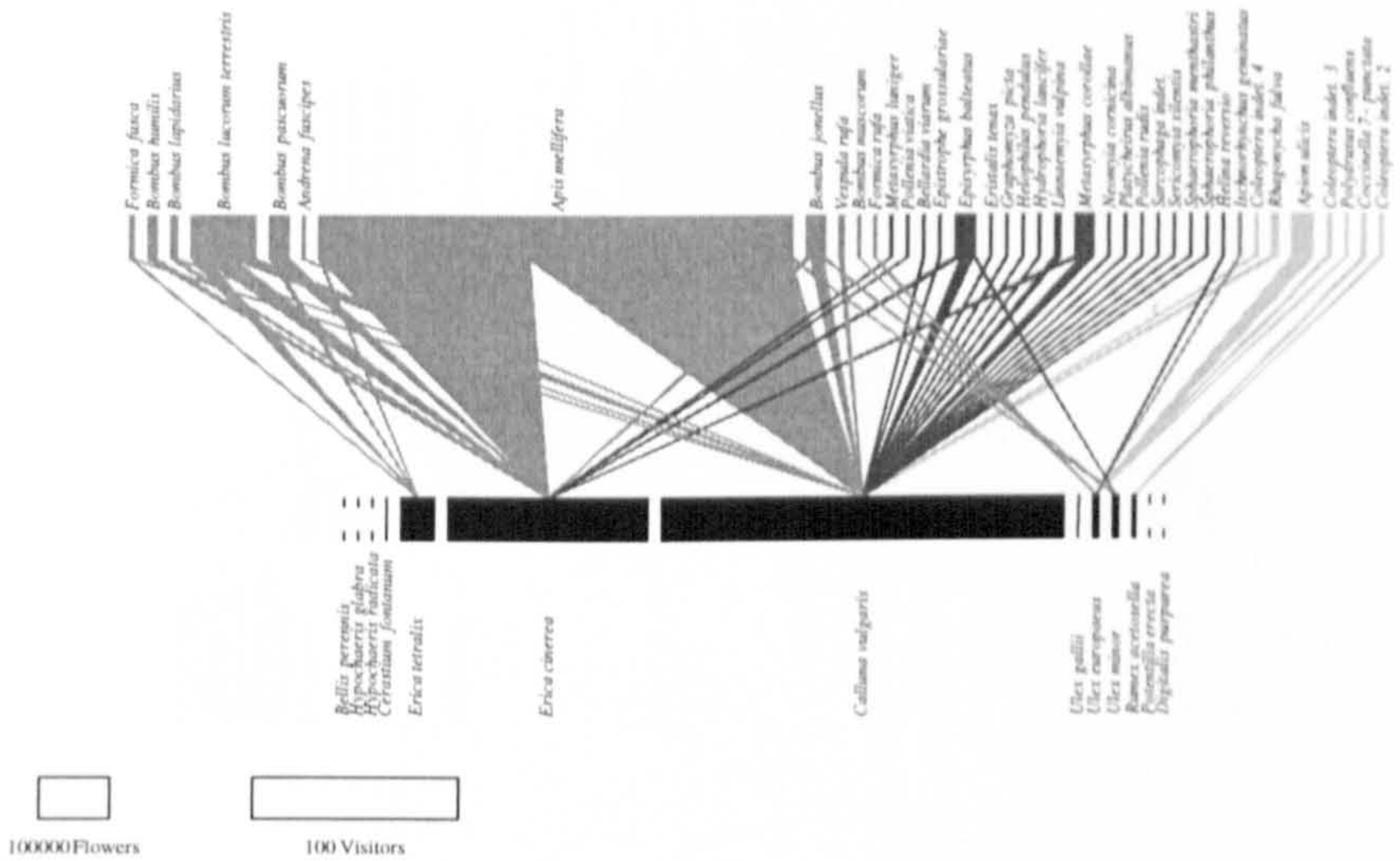


Figure 3.4 Quantitative flower visitation webs for: a) Gore Old and b) Holton Restored. Flower species are shown as rectangles at the bottom of each web, insects are shown above and interactions link plants and insects. The relative abundance of each species is indicated by the width of rectangles and the frequency of each interaction type is indicated by the width of the line. Flower species shown by a stippled line were present on the heathland but not recorded in transects. The different insect orders are shown in different shades of grey. Webs are drawn to the same scale.

(a) Hyde Old

(b) Hyde Restored

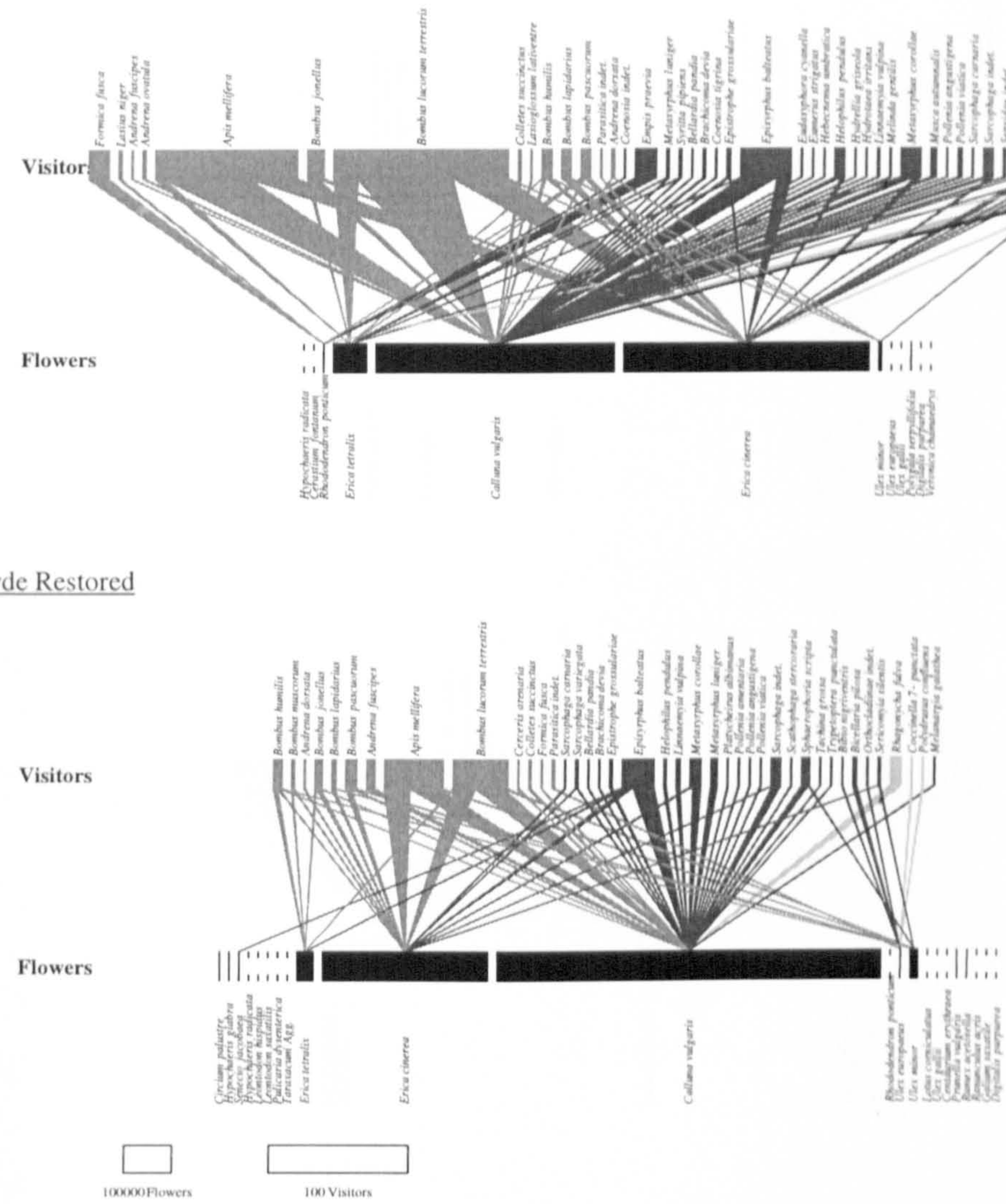
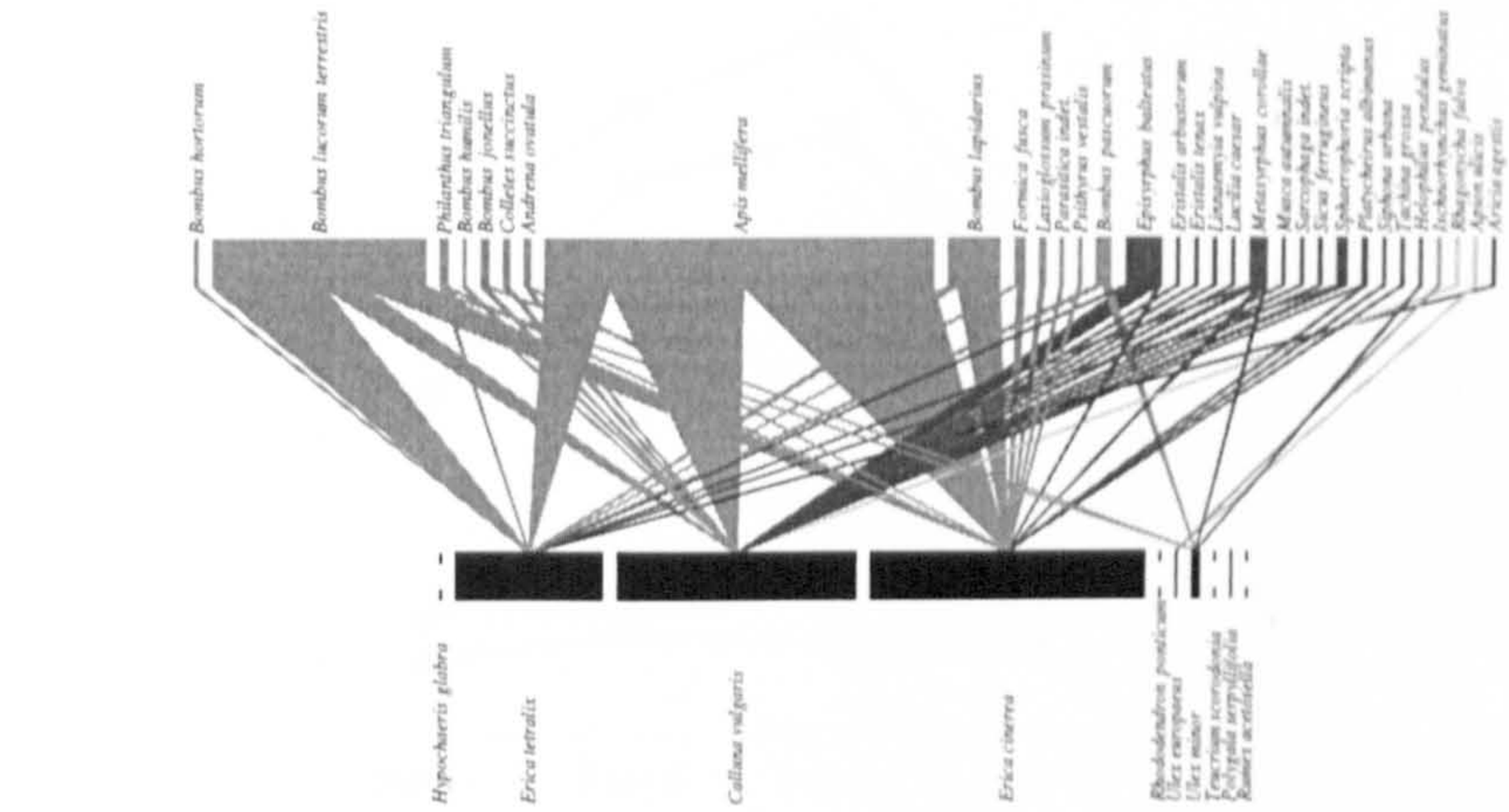


Figure 3.5 Quantitative flower visitation webs for: a) Hyde Old and b) Hyde Restored. Flower species are shown as rectangles at the bottom of each web, insects are shown above and interactions link plants and insects. The relative abundance of each species is indicated by the width of rectangles and the frequency of each interaction type is indicated by the width of the line. Flower species shown by a stippled line were present on the heathland but not recorded in transects. The different insect orders are shown in different shades of grey. Webs are drawn to the same scale.

(a) Morden Old



(b) Morden Restored

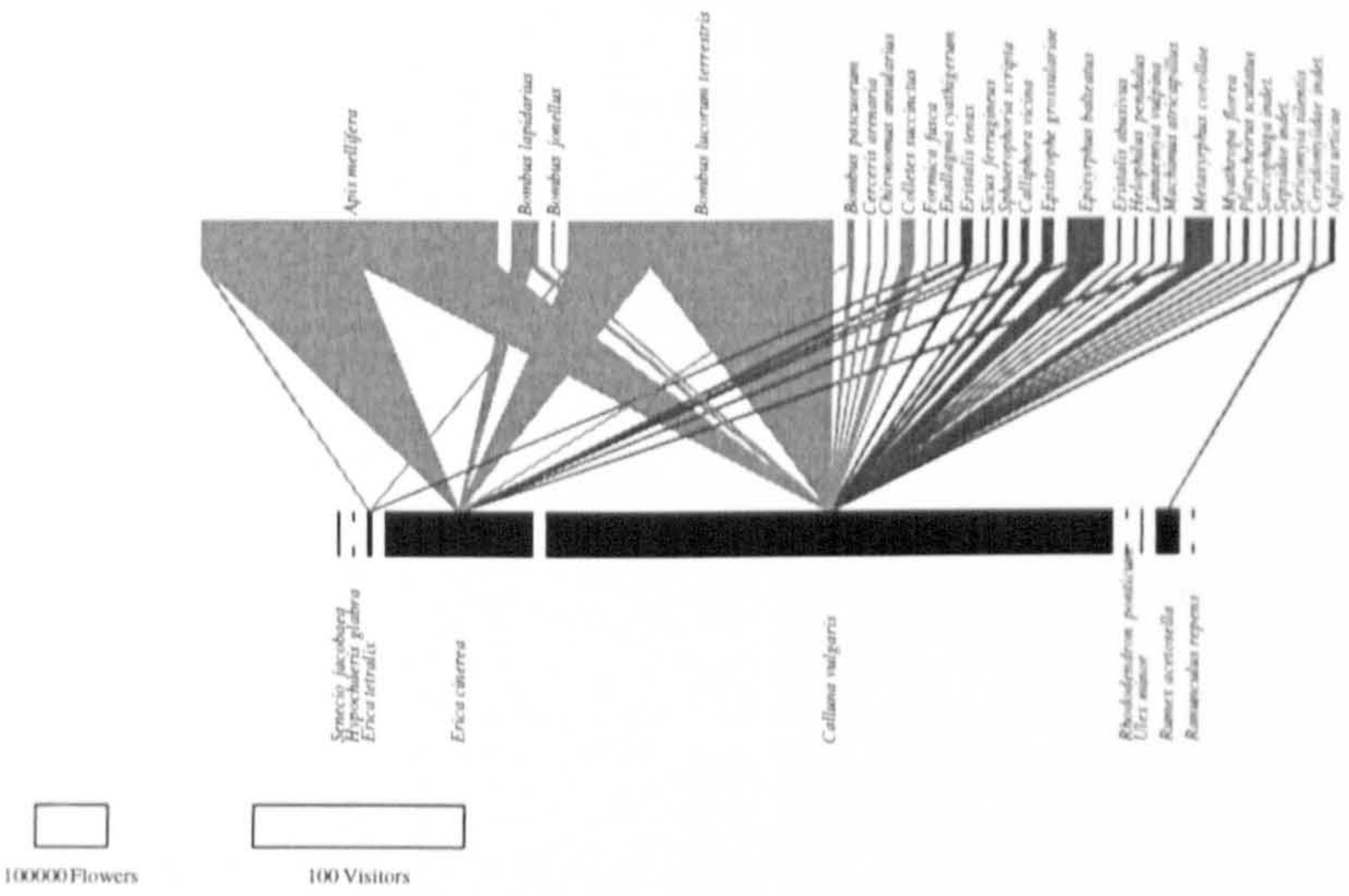


Figure 3.6 Quantitative flower visitation webs for: a) Morden Old and b) Morden Restored. Flower species are shown as rectangles at the bottom of each web, insects are shown above and interactions link plants and insects. The relative abundance of each species is indicated by the width of rectangles and the frequency of each interaction type is indicated by the width of the line. Flower species shown by a stippled line were present on the heathland but not recorded in transects. The different insect orders are shown in different shades of grey. Webs are drawn to the same scale.

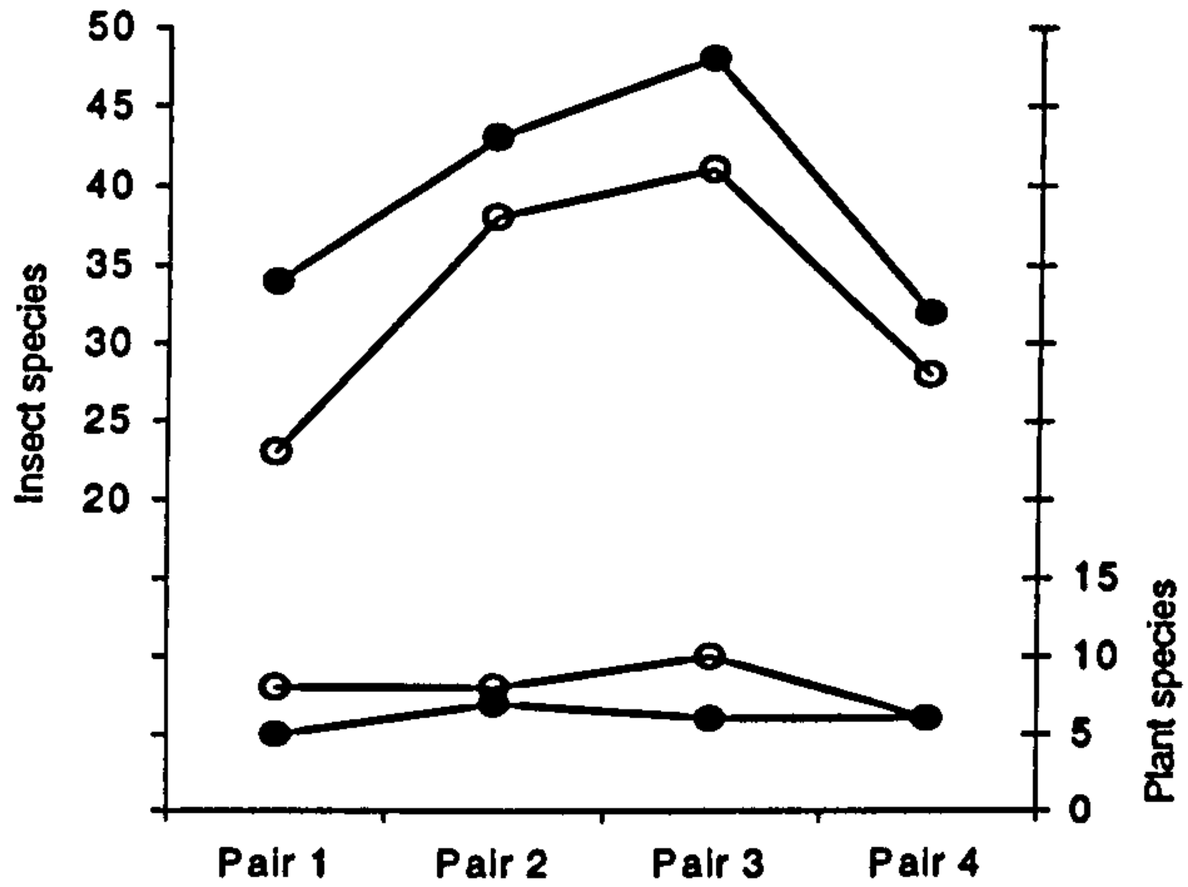
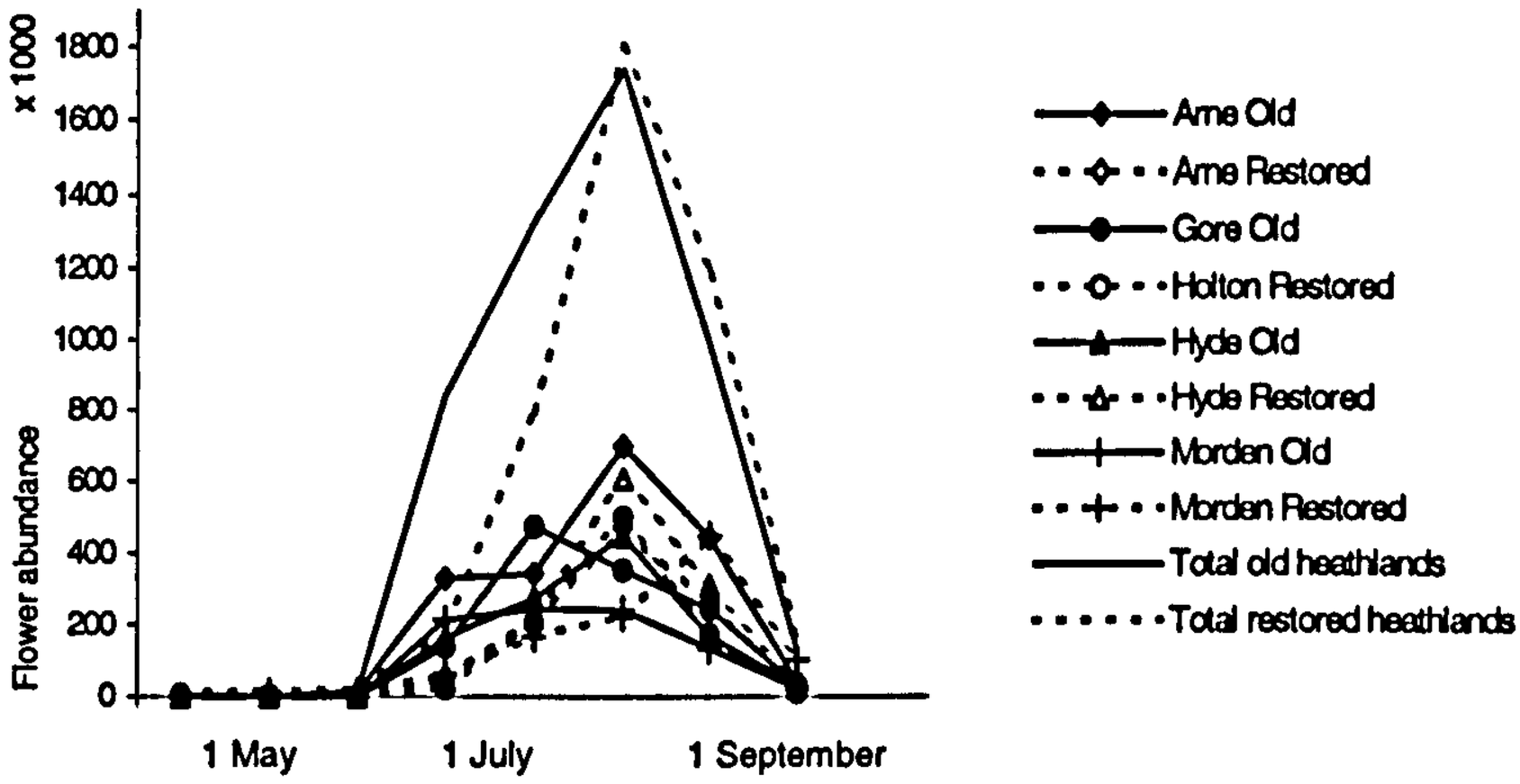
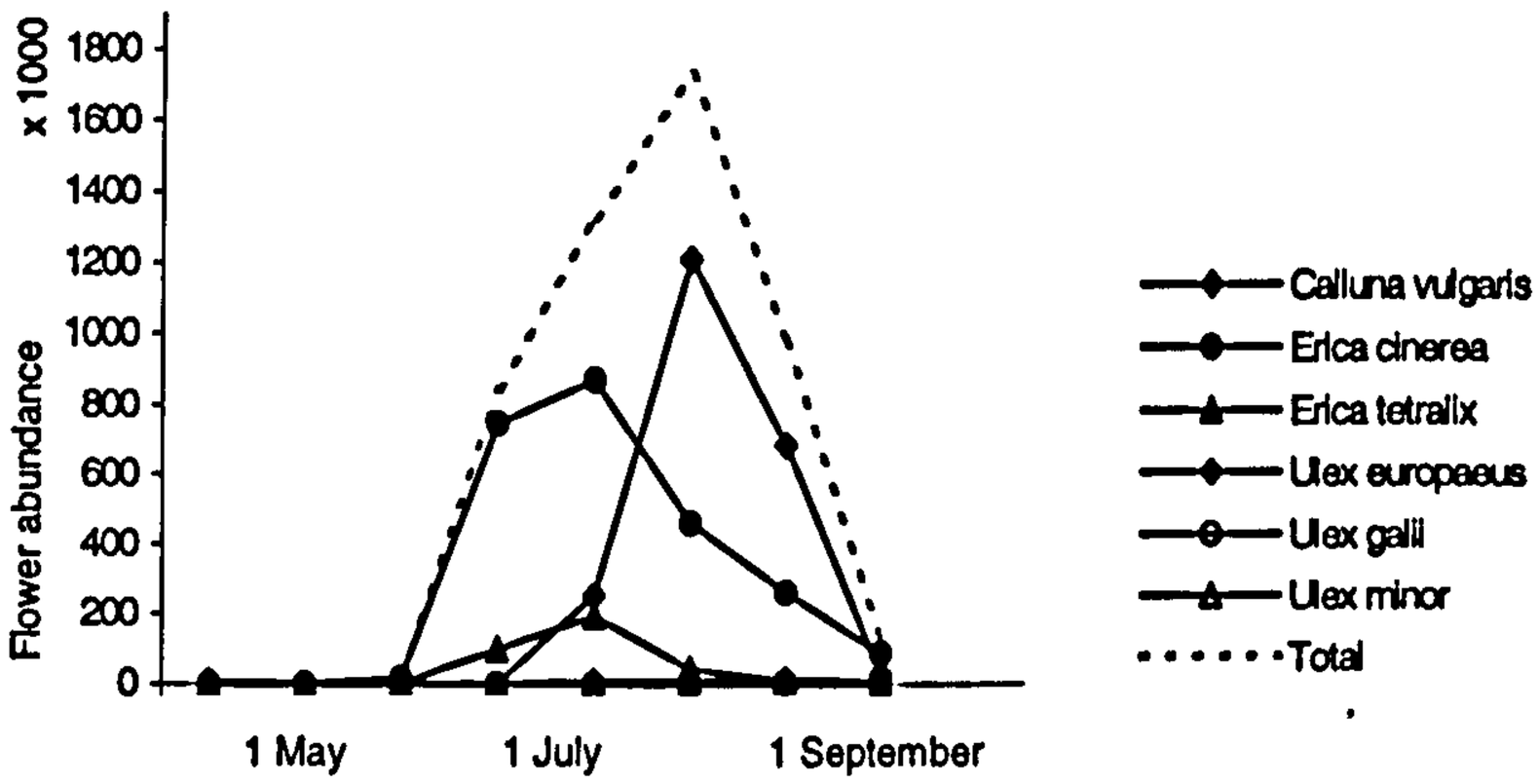


Figure 3.7 Plant and insect species richness on the old (●) and restored (○) heathlands, respectively.

(a)



(b)



(c)

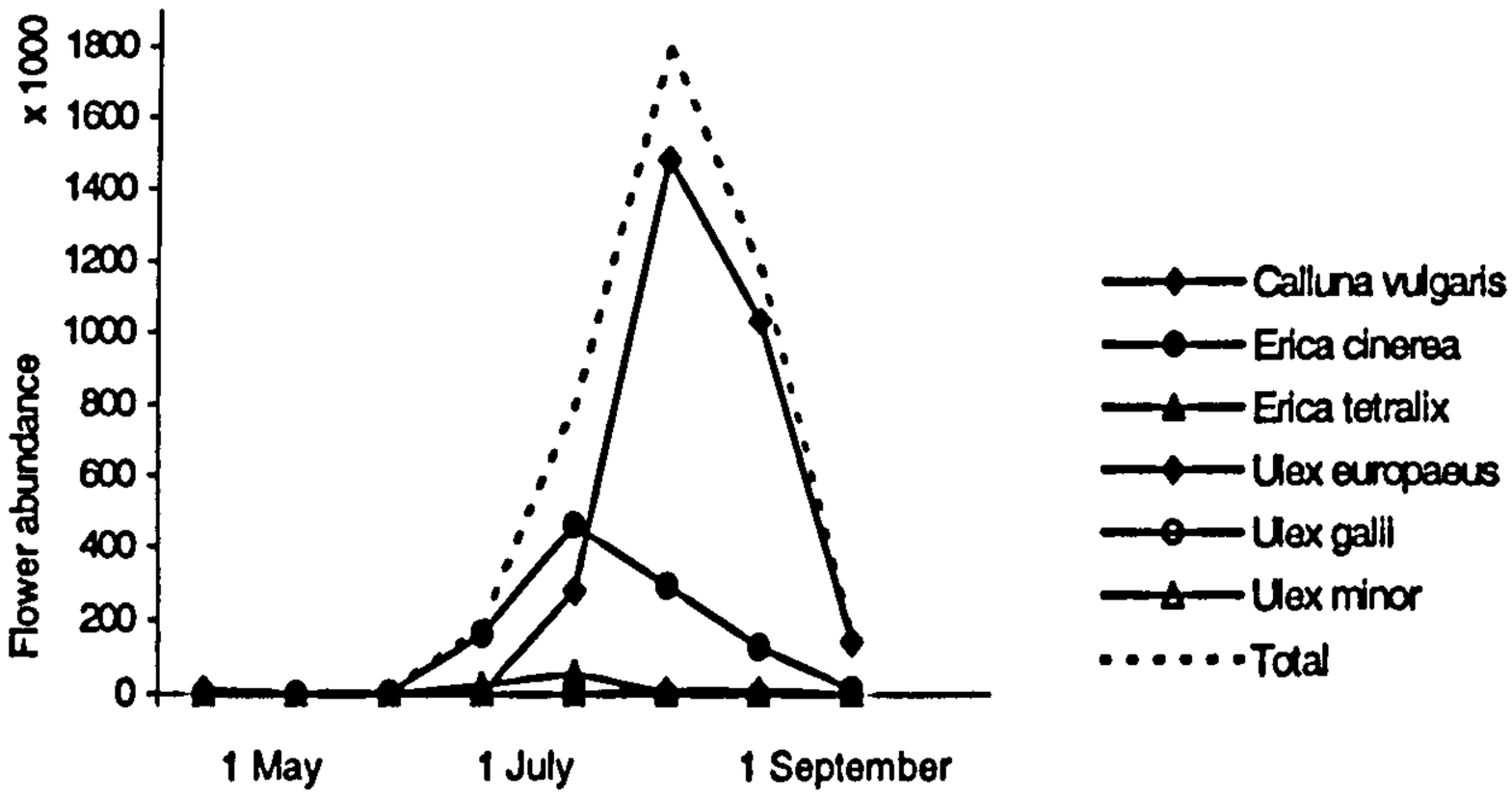
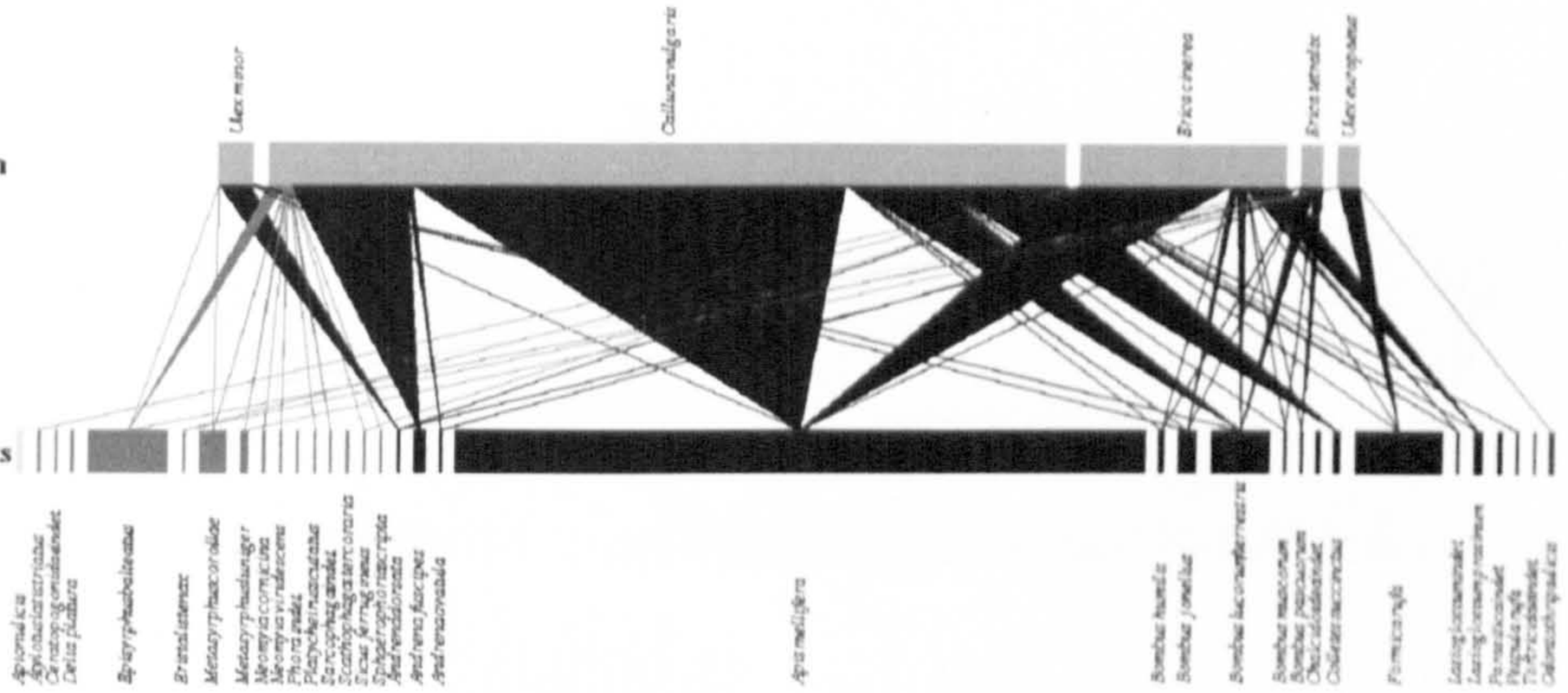


Figure 3.8 Flower abundance per 200 m^2 transect on 8 dry lowland heathlands in 2001. (a) A plot of the floral abundance at each study site, (b) a plot showing the floral composition on old heathlands, (c) a plot showing the floral composition on restored heathlands.

(a) Arne Old



(b) Arne Restored

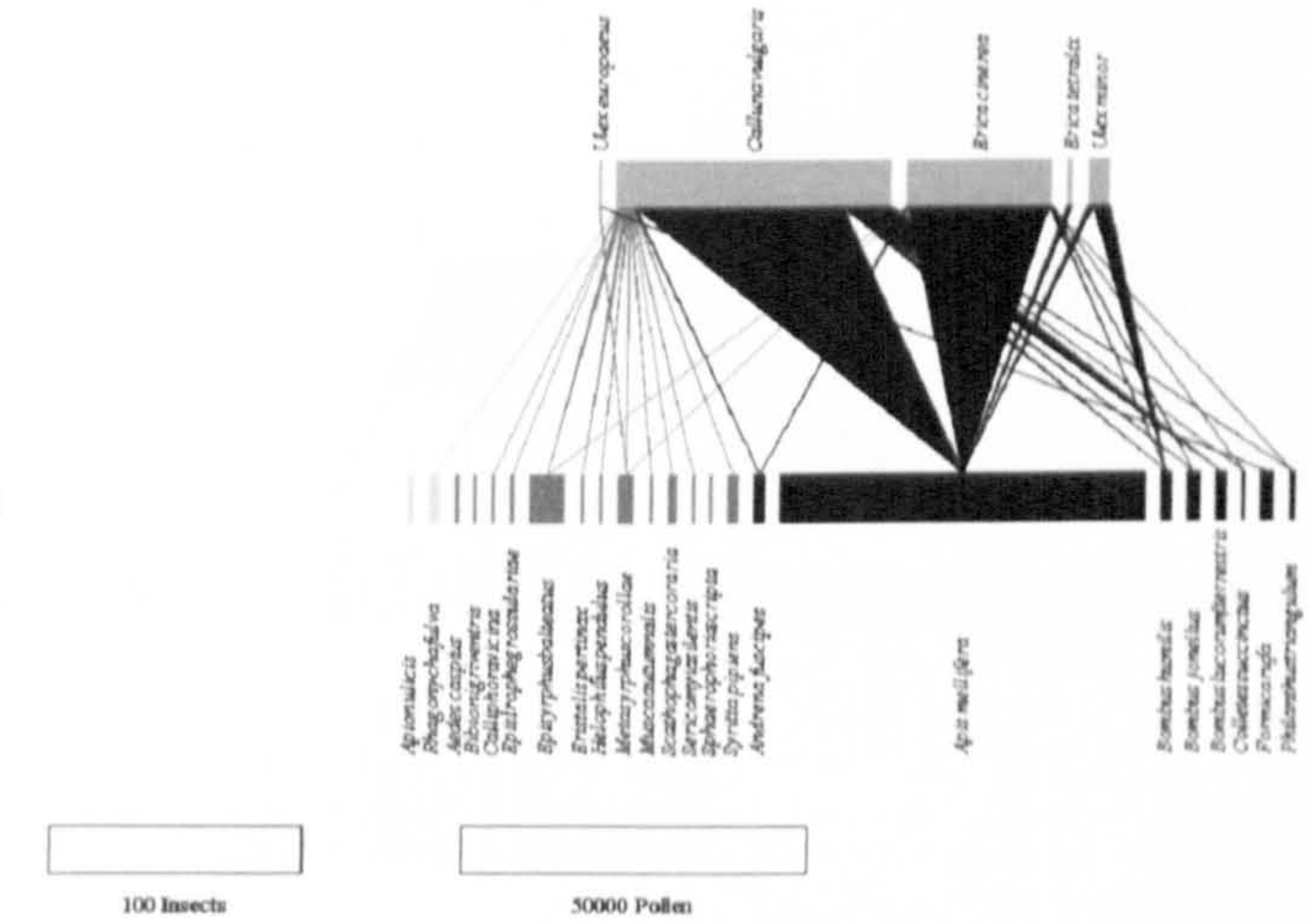
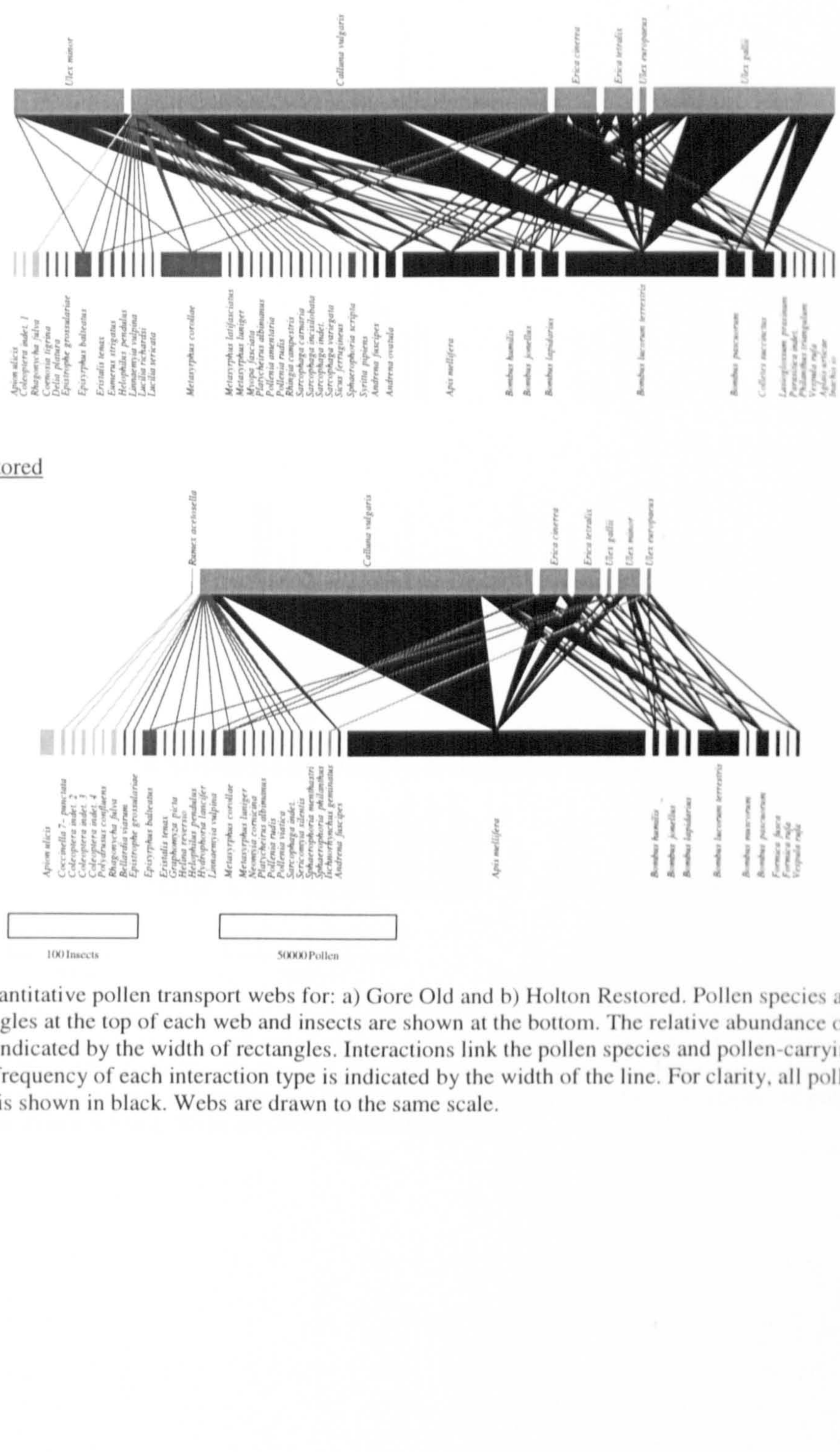


Figure 3.9 Quantitative pollen transport webs for: a) Arne Old and b) Arne Restored. Here pollen species are shown as rectangles at the top of each web, while insects are shown at the bottom. The relative abundance of each species is indicated by the width of the rectangles. Interactions link the pollen species and pollen-carrying insects and the frequency of each interaction type is indicated by the width of the line. For clarity, all pollen carried by bees is shown in black. Webs are drawn to the same scale.

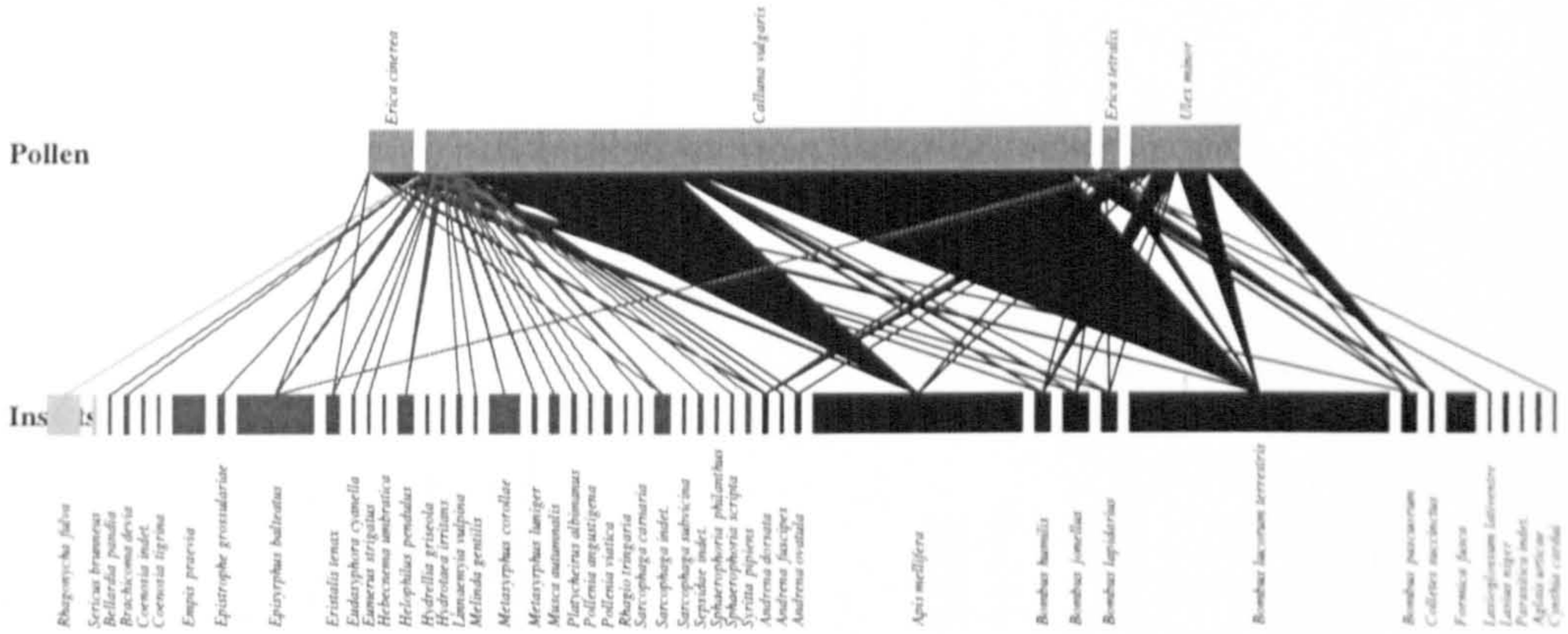
(a) Gore Old



(b) Holton Restored

Figure 3.10 Quantitative pollen transport webs for: a) Gore Old and b) Holton Restored. Pollen species are shown as rectangles at the top of each web and insects are shown at the bottom. The relative abundance of each species is indicated by the width of rectangles. Interactions link the pollen species and pollen-carrying insects and the frequency of each interaction type is indicated by the width of the line. For clarity, all pollen carried by bees is shown in black. Webs are drawn to the same scale.

(a) Hyde Old



(b) Hyde Restored

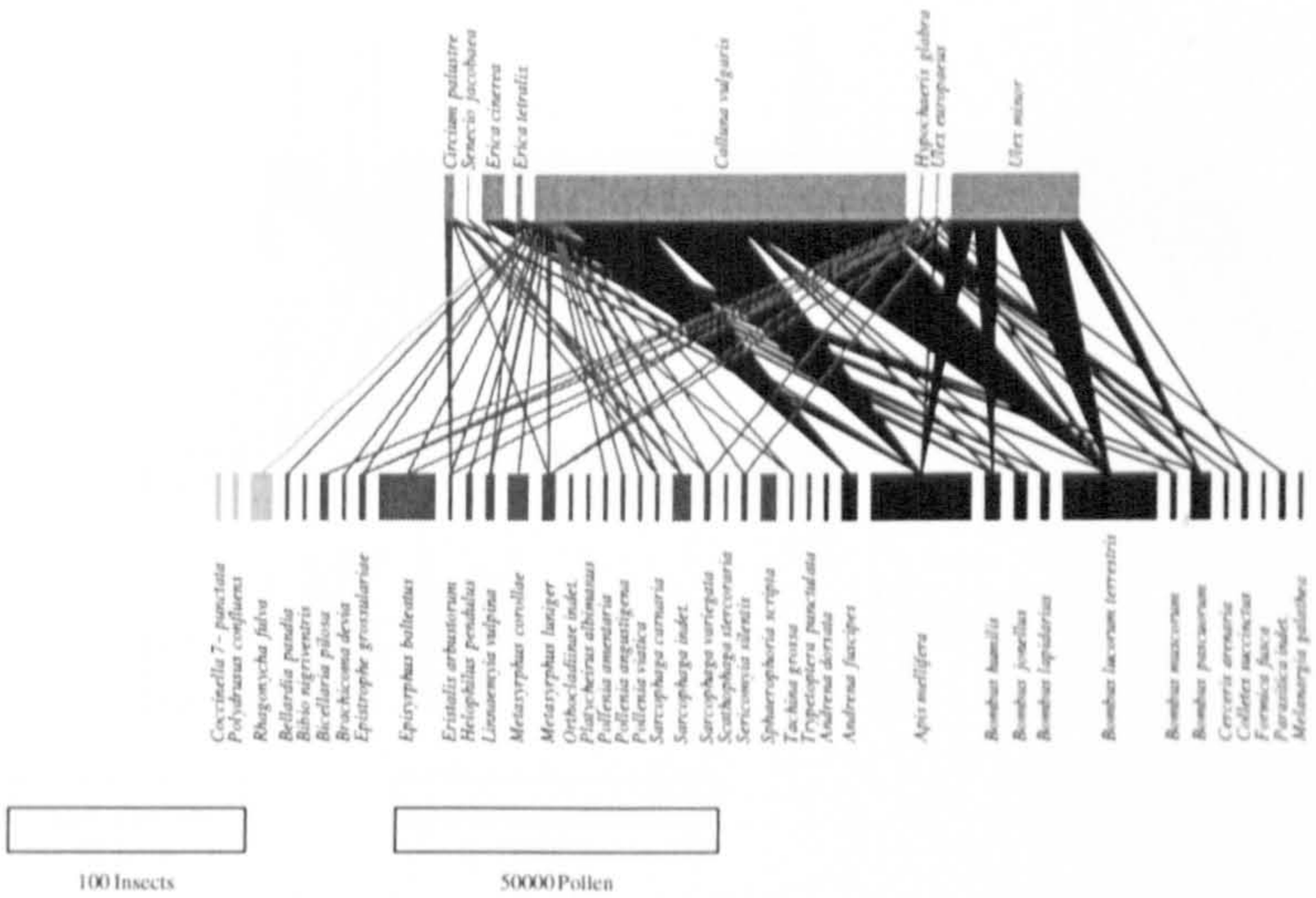
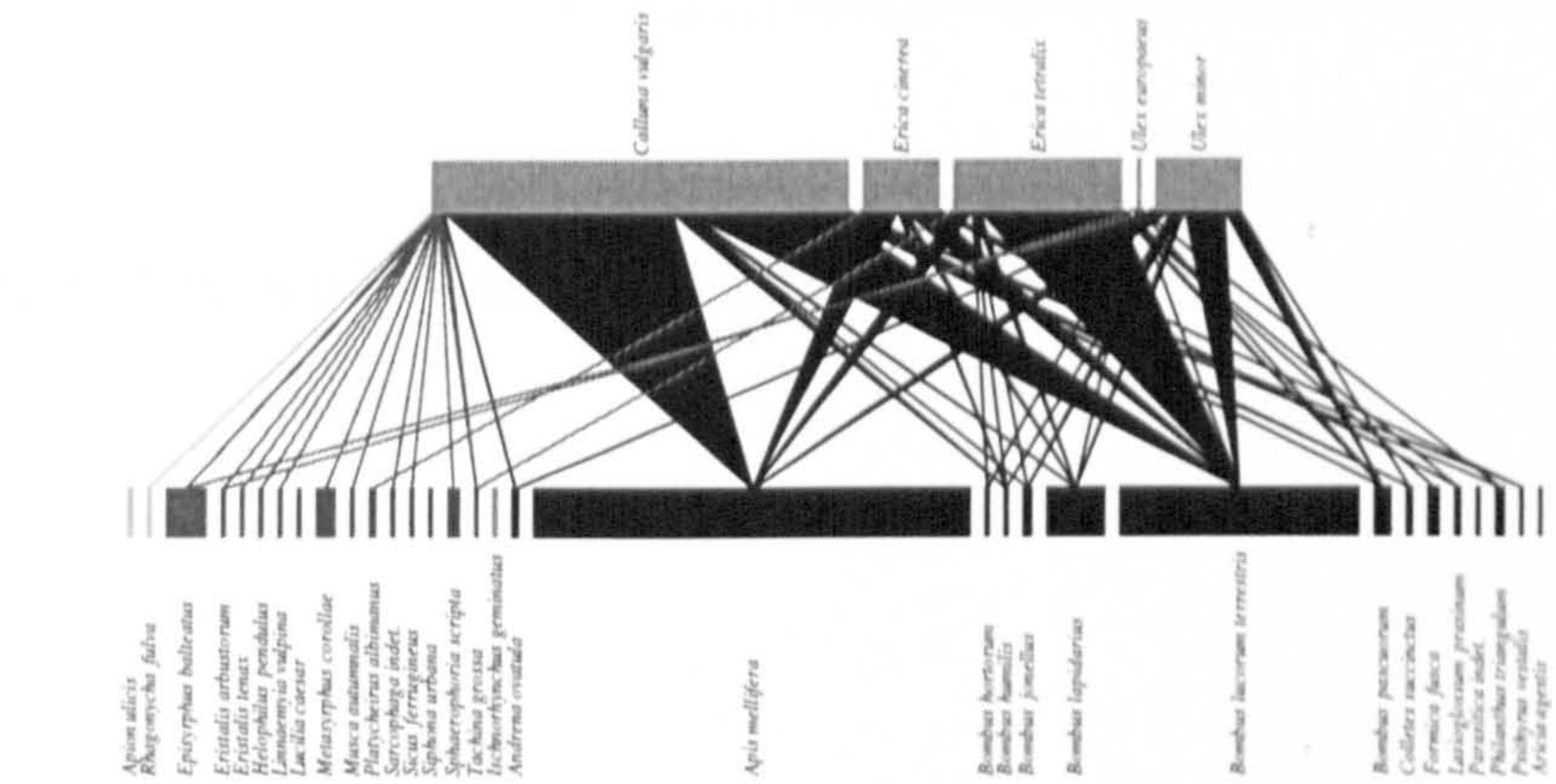


Figure 3.11 Quantitative pollen transport webs for: a) Hyde Old and b) Hyde Restored. Pollen species are shown as rectangles at the top of each web and insects are shown at the bottom. The relative abundance of each species is indicated by the width of rectangles. Interactions link the pollen species and pollen-carrying insects and the frequency of each interaction type is indicated by the width of the line. For clarity, all pollen carried by bees is shown in black. Webs are drawn to the same scale.

(a) Morden Old



(b) Morden Restored

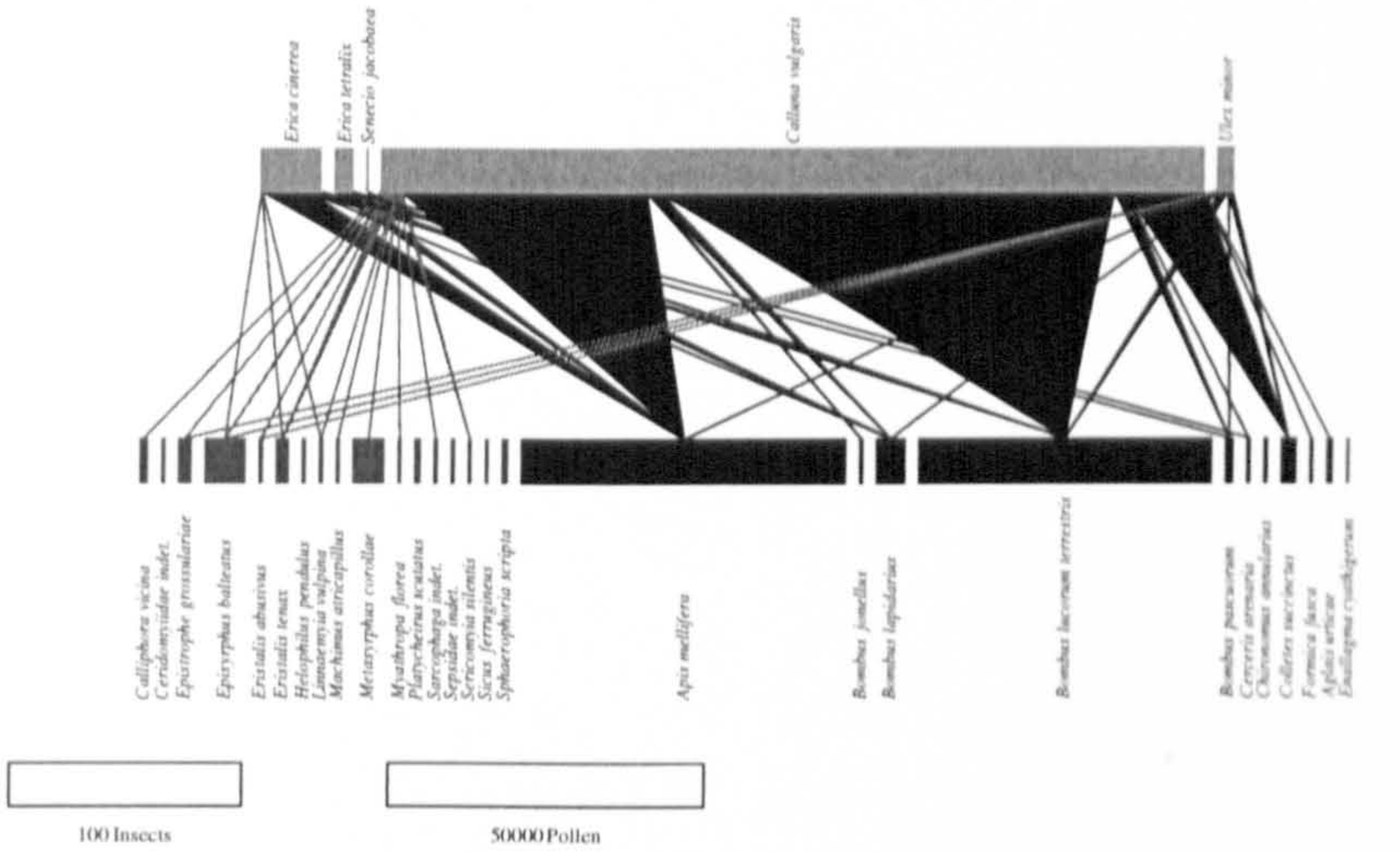


Figure 3.12 Quantitative pollen transport webs for: a) Morden Old and b) Morden Restored. Pollen species are shown as rectangles at the top of each web and insects are shown at the bottom. The relative abundance of each species is indicated by the width of rectangles. Interactions link the pollen species and pollen-carrying insects and the frequency of each interaction type is indicated by the width of the line. For clarity, all pollen carried by bees is shown in black. Webs are drawn to the same scale.

CHAPTER FOUR

Compartmentalization in heathland webs

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Compartmentalization in heathland webs

SUMMARY

If species in a food web interact more strongly with each other than they do with other species, they are said to form a compartment. Only recently has compartmentalization analysis been applied to pollination webs. Here I have taken the analysis one step further and not only consider the visitation interactions but also the pollen transport interactions for 8 lowland heaths. Overall, 48 analyses were carried out. Evidence was found for compartments in some of these webs that corresponded to floral morphology: flies were associated with Calluna vulgaris, *an open and easily accessible flower, while bees were associated with the less accessible flowers* Erica cinerea, Erica tetralix *and the* Ulex *species. Overall, however, compartments were not common in the heathland webs. This is concluded to be partly a failure of Raffaelli and Hall's (1992) method to detect very small compartments, and partly a true feature of these predominantly generalized heathlands.*

4.1 INTRODUCTION

4.11 Compartments in food webs

Pimm & Lawton (1980) stated that "ecological communities persist in the real world despite, not because of, their complexity." They based this on May's models, which predicted that as food webs became larger and more complex, they should also become less stable (May 1972; May 1974). However, May's models also showed that, given average interaction strength and web connectance, the presence of 'blocks' or 'compartments' should increase food web stability. Although Pimm (1982) later found that the presence of blocks reduced stability, workers have searched for the evidence of compartmentalization in real food webs (e.g. Pimm and Lawton 1980; Schoenly 1991; Raffaelli and Hall 1992; Memmott *et al.* 1994; Fonseca and Ganade 1996; Dicks *et al.* 2002). Pimm & Lawton (1980) found evidence for subsystems in some of the 12 webs they investigated but concluded that compartmentalization was probably not a common phenomenon. Since they considered Pimm & Lawton's (1980) method unsuitable for large food webs, Raffaelli & Hall (1992) produced a new method for detecting compartments and went on to re-analyse the 12 webs in Pimm and Lawton (1980) as well as one of their own. They found evidence for compartmentalization in three webs and a general agreement with the results in Pimm and Lawton (1980).

Pimm & Lawton (1980) were concerned that observers of real food webs stop recording where nature provides a convenient natural compartment. They gave as an example a study on oak leaf galls and the interactions between producers, lodgers and enemies. Here a biologist could have sampled individual webs and argued that they represent real compartments, although it would be more appropriate to sample the entire oak-gall system, in which case compartments might not be found, because species could be found interacting with other species elsewhere. Therefore, care must be taken when selecting a suitable habitat type for compartmentalization analysis.

Quantitative flower-visitation data in the style of Dicks *et al.* (2002) and Memmott (1999) provide good opportunities for compartmentalization studies, because these webs nearly represent the complete system of flowers and their insect visitors, albeit with bias towards large day-flying insects. Indeed, Dicks *et al.* (2002) applied the method of Raffaelli

and Hall (1992) to an analysis of flower-visitation webs from a restored and an ancient hay meadow, respectively, and they found evidence for compartmentalization in both webs.

4.12 Compartments in pollination webs

Corbet (2000) suggested that attention should focus on compartments in pollination webs as a means of quantifying which interactions are most at risk. She claimed that *Bombus hortorum* and *Bombus pascuorum* are now the only effective pollinators in the long-tongued bumblebee/deep-corolla flower compartment, because several other long-tongued bee species have declined or disappeared from Western Europe. However, Dicks *et al.* (2002) failed to find such a compartment in their analysis of meadow pollination webs, but ascribed this to the fact that since plants are more generalized than insects, the actual range of compartments is reduced because insects are forced to forage on the available flower types, some of which may not be ideally suited to them.

Quantitative visitation webs are primarily interesting because they elucidate the feeding patterns of the pollinators. However, they do not illustrate how useful the insect visitors are as plant pollinators. Quantitative pollen transport webs are one step closer to this, since they show which pollen species are carried by the different insect species and in what quantity. Because insects vary hugely in how much pollen they carry on their bodies, it is possible that a compartment in a visitation web does not turn out to exist in the pollen transport web.

This paper investigates the presence of compartments in the heathland flower visitation and pollen transport webs, which were presented in Chapter 3. The data are suitable for answering four questions: 1) are heathland flower visitation webs compartmentalised? 2) If they are, do pollen transport webs also show the same compartments as the flower visitation webs? 3) Are compartments similar among replicate webs? And 4) if compartments are inherent features of these heathland webs, have they been reinstated during the 10 years following restoration?

4.2 METHODS

4.21 The 4-step compartmentalization analysis

The analysis followed that of both Raffaelli and Hall (1992) and Dicks *et al.* (2002). It consisted of four steps: 1) an investigation into the shapes of the frequency distribution of trophic similarity curves; 2) correspondence analyses on the quantitative data; 3) analyses of variance on the dimension scores of compartments identified in the ordinations; and 4) comparisons of mean trophic similarity values within and between compartments.

4.22 Step 1: trophic similarity

Trophic similarity, as represented by the Jaccard similarity coefficient, S_{ij} (Jaccard 1912), was calculated between all pairs of plant species and all pairs of insect species in both the visitation and pollen transport webs using the equation:

$$S_{ij} = \frac{a}{a+b+c} \qquad \textbf{Equation 4.1}$$

where a is the number of species involved in interactions with both species i and j; b is the number of species involved in interactions with i only; and c is the number of species involved in interactions with j only. If the web has compartments, the frequency distribution of S_{ij} values is expected to be bimodal or polymodal, because pairs of species within compartments have high S_{ij} values, while pairs of species not in the same compartment have low S_{ij} values. A web with no compartments is expected to show a unimodal distribution. The modality is calculated as the number of peaks above the average frequency for that distribution.

Trophic similarity indices were calculated only for pairs of plant species and pairs of insect species. They were not calculated for pairs containing one plant and one insect species, because in these two-tier webs, species in different trophic levels can have no shared interactions (Dicks *et al.* 2002). Only plant species which were visited during sampling were considered in the analysis. Rare insect species recorded with fewer than 5 specimens were excluded from the analysis as were all pollen transport interactions involving less than 5 grains of a given plant species.

In the distribution, the number of peaks will depend on the number of size classes used (Raffaelli and Hall 1992). Therefore, small webs with few matrix elements may have a

discontinuous distribution of S_{ij} values and this will result in polymodality if a large number of size classes are used. Raffaelli and Hall (1992) solved this problem by devising a standardising scale in which smaller webs are viewed with a smaller number of similarity classes than large webs (Table 4.1). Eight of the 16 webs had fewer than 500 matrix elements and were standardised according to the scale in Table 4.1. Webs larger than 500 matrix elements were viewed with 16 classes, similar to Dicks *et al.* (2002).

4.23 Step 2: correspondence analysis

Correspondence analyses (ter Braak 1986) were carried out on the data to investigate how the plant and insect species fall into groups, based on the species they interact with; (Raffaelli and Hall 1992; Dicks *et al.* 2002). This was done both for the quantitative visitation data, the quantitative pollen carrier data and the quantitative pollen transport data. In the latter two, the quantitative pollen carrier data describes how often an insect species was found to carry the pollen of a given plant species, while the quantitative pollen transport data concerns how much pollen was transported by these carriers.

In the ordinations by Dicks *et al.* (2002), units were insect species and inputs were the proportion of visits by each insect species that were to each particular plant species. Dicks *et al.* (2002) used proportional values in order to avoid bias caused by the large differences in the abundance of the plant species and their analysis therefore concentrated on the plants' perspective. However, because the data are proportions, it is also possible to investigate the insects' perspective, i.e. the proportion of visits that each insect species made to the various plant species. The distinction is relevant because the most common visitor to a given plant species may not be making most of its visits to that plant species. Both viewpoints were analysed in the present study. For the quantitative pollen carrier data, variables were the proportional abundance of each pollen transport interaction. This analysis, therefore, was not concerned with the amount of pollen being carried. Rather it investigated how often the various insect species carried the various pollen species. For the quantitative pollen transport data, variables were the proportional abundance of each pollen species that was carried. Consequently, the overall analysis was substantial: 8 visitation webs, 8 pollen carrier webs and 8 pollen transport webs were each analysed from two points of view.

Because many insects carry pollen of more than one plant species, some plant species could be represented in the pollen transport ordinations but not in the visitation ordinations.

In contrast, not all the insect species represented in the visitation ordinations carried enough pollen for them or their carried pollen species to be included in the pollen transport ordinations. Table 4.2 lists the number of plant and insect species included in the correspondence analyses.

If species appeared to group together in the ordinations such potential compartments were brought forward to Step 3.

4.24 Step 3: analysis of variance

Analyses of variance were carried out on the dimension scores between groups identified in the ordinations of the correspondence analyses. In the 48 analyses, the first two dimensions accounted for an average of 89.5% of the inertia (median = 90.5%, range = 68% - 100%) and although Dimension 1 with an average of 65.17% (median = 59.5%, range = 34% - 100%) accounted more variation than Dimension 2, both dimensions were used for separating out the possible groupings, similar to Dicks *et al.* (2002). Where the data violated the assumptions of normality and homoscedasticity, the data were analysed with the non-parametric Kruskal-Wallis test (Sokal and Rohlf 1995). If the scores of one group were different from those of the other groups in at least one dimension, this group was brought forward to Step 4. Some groups were too small for analysis and were ignored. The potential inability of the analysis to detect small compartments is an acknowledged problem (Raffaelli and Hall 1992). If there was a suggestion that small compartments occurred in the heathland webs, these were considered separately.

4.25 Step 4: Within and between group trophic similarities

We would expect species in true web compartments to share many interactions. Therefore, if groups which were identified in the ordinations and confirmed in the analyses on the ordination scores represent true web compartments, the trophic similarity values should be higher among species within these groups than between species in different groups. Consequently, trophic similarity values were compared within and between groups using t-tests where the data followed assumptions of normality and homoscedasticity (Sokal and Rohlf 1995). Where this was not the case, the Mann-Whitney U-test was used instead. Small groups could not be analysed in this way. However, since even a small number of S_{ij}-values constitutes the entire population of S_{ij}-values for a given group, the range of similarity values between groups was investigated to see if it included the value or values

of the within-group S_{ij} distribution. If this was not the case, the small group was concluded to be significantly different. As before, very small groups consisting only of one insect species and one plant species had no trophic similarity value and could not be analysed this way. For these groups, I conservatively defined the two species to be a compartment only if their similarity values with other species in the web were no higher than 0.25 and if at least 75% of their interactions were with each other.

4.3 RESULTS

4.31 Trophic similarities

Table 4.3 shows that the visitation webs were always larger than the pollen transport webs. This is partly an effect of excluding from the analysis all rare interactions or interactions in which a pollinator moved less than 5 grains of a given plant species. All webs showed polymodality and thus evidence of possible compartmentalization. Figure 4.1 is an example of the frequency distributions and shows the Arne Old visitation and pollen transport data, respectively.

4.32 Compartments

Only 10 compartments were identified in the 48 analyses and only 4 of the 8 heathlands had at least one compartment in either of the visitation data, the pollen carrier data or the pollen transport data. 6 compartments were found in the data as seen from a plant point of view, while only 4 compartments were found from an insect point of view. Figure 4.2 shows two examples of ordinations from the correspondence analyses. The compartments are shown in Table 4.4 and Table 4.5.

Hoverflies and solitary bees only occurred in compartments with *Calluna vulgaris*, while *Apis mellifera* and the *Bombus* species were more catholic. In the few compartments without *Calluna* (in webs for Hyde Restored), hoverflies and solitary bees were absent, while the social hymenoptera were common.

Table 4.4 shows the plant perspective on compartments for which within-group trophic similarity indices were significantly different from between-group similarity scores. In the visitation data, a compartment was identified only on one heathland, Hyde Old. For the pollen carrier data, compartments were only identified for three heaths: Arne Restored, Gore Old and Hyde Restored. Only two pollen transport compartments were identified, both on Hyde Restored. The compartments were relatively large subsets of the webs, ranging from between 30.00% (Arne Restored: pollen carriers) to 76.47% (Gore Old: pollen carriers) of the species.

Table 4.5 shows the insect perspective on compartments. In the visitation data, compartments were identified only in two webs: Hyde Old had two compartments and Hyde Restored had one. Similarly, for the pollen carrier data, compartments were only

identified in the webs for Hyde Old and Hyde Restored, where each had one compartment. None were identified in the pollen transport webs. Compared to those of the plant perspective, the insect perspective compartments were smaller subsets of the webs but still ranged from between 25.00% (Hyde Restored: pollen carriers) to 52.63% (Hyde Old: visitation) of the species.

4.33 Pairs of species

Table 4.6 and Table 4.7 show the possible single-species pair compartments, which were identified in the correspondence analyses, from the points of view of the plants and insects, respectively. No pair passed the conservative criteria for compartmentalization.

4.34 Multiple compartments within sites

Hyde Old had 2 visitation compartments: one from an insect point of a view and one from a plant point of view. These two were almost identical and all the species of the former were also present in the latter. They included the plants *Calluna vulgaris* and *Erica tetralix* as well as species of hoverflies and social bees. From the plant point of view, one of both these types of insect was included: *Eristalis tenax* and *Bombus pascuorum*. A reduced version of the insect compartment was translated into a pollen carrier compartment for Hyde Old. Here *Calluna* grouped with both another plant species, *Cirsium palustre*, as well as with three species of hoverfly, with which it had also grouped in the visitation data.

For Hyde Restored, a visitation compartment (insect perspective), which included *Erica cinerea* and *Ulex minor*, *Apis mellifera* and three species of *Bombus*, was poorly translated into a pollen carrier compartment with *E. cinerea* and *E. tetralix*, besides *Bombus humilis* and *Bombus jonellus*. Here only *E. cinerea* and *Bombus jonellus* had also grouped together in the visitation compartment. However, both species also grouped together in a pollen transport compartment (plant perspective) for that same heath.

4.35 Old and restored compartments

Compartments were found in both the old and the restored heathlands of only one pair: Hyde Old and Hyde Restored. However, there were few similarities. For example, in the visitation webs (plant perspective) *Apis mellifera* and *Bombus lucorum/terrestris* grouped with *Calluna vulgaris* and *Erica tetralix* on the old heathland, whereas they grouped with *Erica cinerea* and *Ulex minor* on the restored heathland.

4.4 DISCUSSION

In this section I first review the evidence of compartmentalization in the heathland webs. I will then explain the pattern of few emerging compartments with particular reference to heathlands as highly generalised pollination systems and the limitations of the current approach.

4.41 Compartments in heathland webs

With only 10 compartments identified in 48 analyses, it must be concluded that compartmentalization in heathland plant-pollinator webs is an atypical and, perhaps, a partially random occurrence. Moreover, the two viewpoints made little difference, but showed similar species associations in webs where both viewpoints yielded compartments.

4.42 Why are compartments uncommon on heathlands?

It is a matter of contention whether generalization in food webs increases with the number of species (e.g. Havens 1993; Ollerton and Cranmer 2002). However, heathlands are unusually low in plant species but also rich in insect species; therefore generalization should be particularly common on the heathlands, because so many insect species feed on the same few plant species. Indeed this was found in the present work, but more small compartments were expected because, in particular, the *Ulex* species invite a higher degree of specialization. For example, the solitary bee *Andrena ovatula* could form such compartments with species of *Ulex*, although this was not confirmed in the present study. Moreover, it is possible that where very big compartments were found, e.g. the pollen carrier compartment on Gore Old (plant perspective) that encompassed 5 of the 7 plant species and 8 of the 10 insect species, this reflected not such much a real compartment as it reflected compartments in the four remaining species. Ordination suggested that these could form separate compartments (Figure 4.2) with *Hypochaeris glabra* and *Metasyrphus corollae* forming one compartment and *Ulex europaeus* and *Andrena ovatula* forming another. However, neither compartment passed the conservative test criteria.

The failure to pick out small compartments could be due to a combination of both the problem with the method and a problem associated with using data from an entire season. For example, insect species may form temporal or successive compartments, e.g. with *Ulex* species when these are in bloom, but feed on *Erica* species at other times. Because they would then temporarily join a highly generalised pollinator community, the strong

interaction with *Ulex* species could be obscured in the amalgamated data. It would be interesting to sample a heathland more intensively over the season to see if insects do indeed switch compartments.

4.43 Observed compartments

Were the few identified compartments representative of ecological groupings? Although some compartments saw a combination of both, there was a trend of *Calluna vulgaris* being associated with flies, while *Erica cinerea*, *Erica tetralix* and *Ulex minor* were associated with bees. To a large degree, this reflects flower morphology and confirms that flies prefer open, easily accessible flowers, whereas bees can handle more complex flowers.

The corolla tubes of the two *Erica* species are too long for most flies to harvest any nectar legitimately, and flies are not known to be either primary or secondary nectar robbers (Maloof and Inouye 2000). In contrast, the short-tongued *Bombus lucorum/terrestris* is often associated with nectar robbing (Maloof and Inouye 2000; Stout *et al.* 2000). Once a hole has been bored at the base of a flower it can be used by other bees as well and nectar robbing was very common in *E. cinerea* (*pers. obs.*). Bumblebees exhibit two major feeding behaviours: pollen gathering and nectar gathering (either by legitimate means or by robbing). When they gather pollen, they are legitimate agents of pollination, but even as nectar robbers, they may transfer pollen to the stigma whilst handling the flower (Maloof and Inouye 2000). Individuals can exhibit both behaviours during a foraging trip (Maloof and Inouye 2000). Moreover, all the flower-visiting bees in the study carried pollen. It is possible that both geitonogamy (the pollination of flowers by pollen from other flowers on the same plant) and outcrossing rates are affected by nectar robbing in complex ways, but this does not appear to be a problem for the very widespread heathland species, *E. cinerea*.

That *U. minor* should be associated with bees is not surprising. *Ulex* species produce no nectar but copious amounts of pollen and have closed flowers, which the pollinators must trip to open. Flies are probably unable to trip *Ulex* flowers and none was seen doing so in the present study, although some hoverflies visited previously tripped flowers. Occasionally, honeybees, *Apis mellifera*, visited *Ulex* flowers, but this was a rare interaction, rather it was bumblebees and *Colletes succinctus* which were the chief visitors of *Ulex*.

4.44 Visitation web and pollen web compartments

What was the relationship among the types of web? Little overlap was evident on the heathlands where compartments were found in both the visitation and pollen webs, although the pollen carrier webs and the pollen transport webs were better related, as might be expected. While the visitation webs could include both *Calluna vulgaris* and the two species of *Erica*, these genera were typically separated in the pollen compartments. This may reflect two factors: firstly that hoverflies are more likely to pick up the pollen of *Calluna* than the pollen of the *Erica* species, because when they land on the former, they can touch the anthers directly, whereas when they land on the tubular *Erica* flowers, their bodies are unlikely to touch the anthers. Secondly, bees are associated with the *Erica*s both because they might prefer these flowers over *Calluna* but also because the *Erica*s start flowering earlier; i.e. the bees had been feeding on and carried pollen of the *Erica*s prior to the flowering of *Calluna*.

4.45 Replication and restoration

One of the more surprising results of this analysis is the considerable variation among the few observed compartments. Despite the trend of flies being associated with *Calluna* and bees with the *Erica*s, the exact composition was highly variable within compartments. This is similar to the findings of Dicks *et al.* (2002) who obtained evidence for compartmentalization at both their study sites and noted a correspondence to the classical pollination syndromes, although the composition of their compartments also varied considerably between their sites. Analogous to the present study, the two study sites of Dicks *et al.* (2002) were an ancient and a restored hay meadow. Therefore, it could be concluded that compartments had been reinstated on the restored meadow. For the heathlands, compartments may be atypical and partially random, but since no difference was found between old and restored heathlands, the restoration can be regarded a success from a compartmentalization point of view.

TABLES

Table 4.1 Standardizing scale for comparison of different webs (from Rafaelli & Hall 1992).

Number of elements in half-matrix of S_{ij} values (web size)	Number of similarity classes in distribution examined
< 100	6
100-150	7
150-200	8
200-250	9
250-300	10
450-500	15

Table 4.2 The number of plant and insects species considered in the correspondence analyses.

	Visitation webs		Pollen transport webs	
	Plant species	Insect species	Plant species	Insect species
Arne Old	5	7	4	6
Arne Restored	3	5	4	4
Gore Old	5	11	7	10
Holton Restored	5	7	5	6
Hyde Old	5	13	7	11
Hyde Restored	5	12	4	10
Morden Old	4	6	5	5
Morden Restored	3	8	4	8

Table 4.3 Web size and modality in frequency distributions for trophic similarity values in 8 quantitative visitation webs and 8 quantitative pollen transport webs.

	Visitation webs			Pollen transport webs		
	Web Size	Similarity classes	Modality (peaks above average)	Web size	Similarity classes	Modality (peaks above average)
Arne Old	538	16	Polymodal (3)	346	11	Polymodal (3)
Arne Restored	259	9	Polymodal (3)	220	9	Polymodal (3)
Gore Old	918	16	Polymodal (3)	517	16	Polymodal (3)
Holton Restored	756	16	Polymodal (4)	336	11	Polymodal (4)
Hyde Old	1138	16	Polymodal (4)	711	16	Polymodal (4)
Hyde Restored	801	16	Polymodal (4)	471	16	Polymodal (4)
Morden Old	506	16	Polymodal (4)	346	11	Polymodal (3)
Morden Restored	384	11	Polymodal (4)	225	11	Polymodal (3)

Table 4.4 Compartments identified where within-groups trophic similarity scores were significantly different from scores between groups. Plant perspective.

Site	Visitation compartments	Pollen carrier compartments	Pollen transport compartments
Arne Old	None	None	None
Arne Restored	None	*Calluna vulgaris* & *Bombus jonellus* and *Episyrphus balteatus*	None
Gore Old	None	*Calluna vulgaris*, *Erica cinerea*, *Erica tetralix*, *Ulex gallii*, *Ulex minor* & *Apis mellifera*, *Bombus humilis*, *Bombus jonellus*, *Bombus lapidarius*, *Bombus lucorum/terrestris*, *Bombus pascuorum*, *Colletes succinctus* and *Episyrphus balteatus*	None
Holton Restored	None	None	None
Hyde Old	*Calluna vulgaris*, *Erica tetralix* & *Apis mellifera*, *Bombus pascuorum*, *Bombus jonellus*, *Bombus lucorum/terrestris*, *Episyrphus balteatus*, *Eristalis tenax*, *Helophilus pendulus*, *Metasyrphus corollae*, *Metasyrphus luniger* and *Rhagonycha fulva*	None	None
Hyde Restored	None	*Calluna vulgaris* & *Andrena fuscipes*, *Episyrphus balteatus*, *Metasyrphus corollae* and *Rhagonycha fulva*	*Calluna vulgaris* & *Andrena fuscipes*, *Episyrphus balteatus*, *Metasyrphus corollae* and *Rhagonycha fulva* *Erica cinerea*, *Erica tetralix* & *Apis mellifera*, *Bombus humilis* and *Bombus jonellus*
Morden Old	None	None	None
Morden Restored	None	None	None

Table 4.5 Compartments identified where within-groups trophic similarity scores were significantly different from scores between groups. Insect perspective.

Site	Visitation compartments	Pollen carrier compartments	Pollen transport compartments
Arne Old	None	None	None
Arne Restored	None	None	None
Gore Old	None	None	None
Holton Restored	None	None	None
Hyde Old	*Calluna vulgaris*, *Erica tetralix* & *Apis mellifera*, *Bombus jonellus*, *Bombus lucorum/terrestris*, *Episyrphus balteatus*, *Helophilus pendulus*, *Metasyrphus corollae*, *Metasyrphus luniger* and *Rhagonycha fulva*	*Calluna vulgaris*, *Cirsium palustre* & *Episyrphus balteatus*, *Helophilus pendulus*, *Metasyrphus corollae* and *Rhagonycha fulva*	None
Hyde Restored	*Erica cinerea*, *Ulex minor* & *Apis mellifera*, *Bombus jonellus*, *Bombus lucorum/terrestris* and *Bombus pascuorum*	*Erica cinerea*, *Erica tetralix* & *Bombus humilis* and *Bombus jonellus*	None
Morden Old	None	None	None
Morden Restored	None	None	None

Table 4.6 Single-pair compartments identified in ordinations but impossible to verify in analyses on trophic dissimilarity with other species, because a pair of one plant and one insect species has no S_{ij} value. Plant perspective.

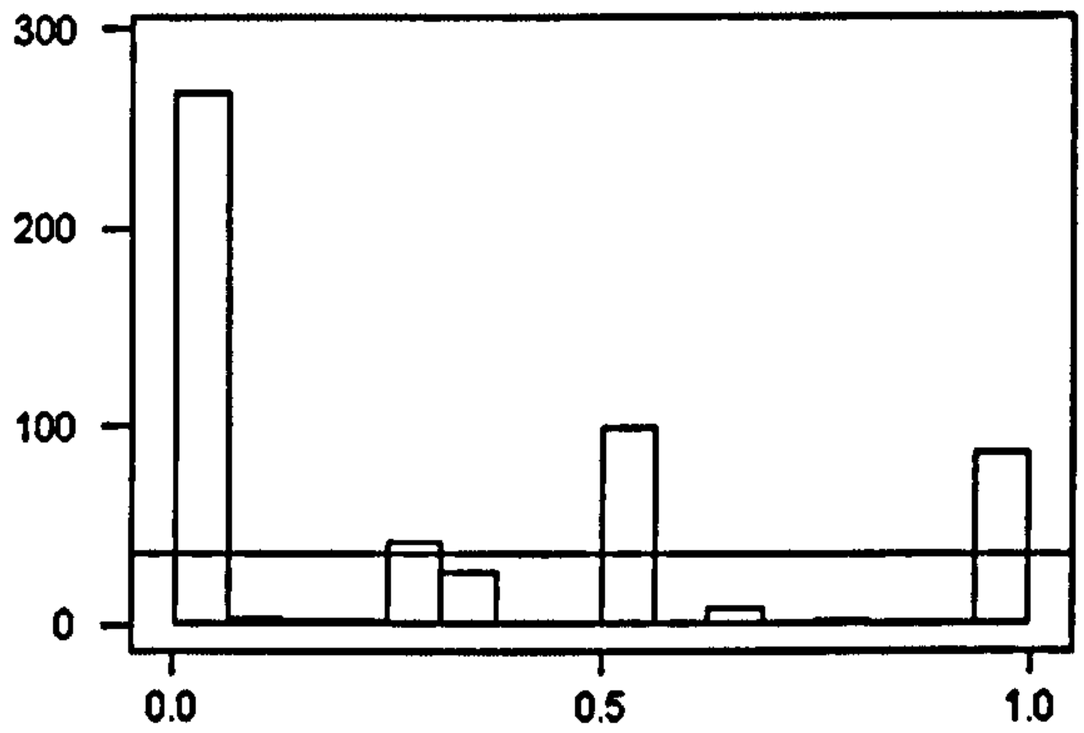
Site	Visitation compartments	Pollen carrier compartments	Pollen transport compartments
Arne Old	*Ulex europaeus* & *Formica rufa* *Ulex minor* & *Bombus lucorum/terrestris*	None	None
Arne Restored	None	None	None
Gore Old	None	*Hypochaeris glabra* & *Metasyrphus corollae* *Ulex europaeus* & *Andrena ovatula*	None
Holton Restored	None	None	*Ulex gallii* & *Bombus lucorum/terrestris*
Hyde Old	None	*Cirsium palustre* & *Helophilus pendulus*	*Hypochaeris glabra* & *Eristalis tenax* *Ulex minor* & *Bombus humilis*
Hyde Restored	None	None	None
Morden Old	None	None	*Erica tetralix* & *Bombus lucorum/terrestris*
Morden Restored	None	None	None

Table 4.7 Single-pair compartments identified in ordinations but impossible to verify in analyses on trophic dissimilarity with other species, because a pair of one plant and one insect species has no S_{ij} value. Insect perspective.

Site	Visitation compartments	Pollen carrier compartments	Pollen transport compartments
Arne Old	*Ulex europaeus* & *Formica rufa*	None	*Erica cinerea* & *Bombus jonellus* *Ulex minor* & *Metasyrphus corollae*
Arne Restored	*Calluna vulgaris* & *Episyrphus balteatus* *Ulex europaeus* & *Formica rufa*	None	*Ulex europaeus* & *Formica rufa*
Gore Old	*Ulex minor* & *Andrena ovatula*	*Ulex minor* & *Andrena ovatula*	None
Holton Restored	*Ulex europaeus* & *Apion ulicis*	*Ulex gallii* & *Apis mellifera*	*Erica cinerea* & *Metasyrphus corollae* *Ulex minor* & *Bombus pascuorum*
Hyde Old	None	*Hypochaeris glabra* & *Eristalis tenax*	None
Hyde Restored	*Erica tetralix* & *Bombus lucorum/terrestris*	None	*Erica cinerea* & *Bombus jonellus*
Morden Old	*Calluna vulgaris* & *Episyrphus balteatus* *Ulex minor* & *Bombus pascuorum*	None	None
Morden Restored	None	*Ulex minor* & *Bombus lucorum/terrestris*	*Ulex minor* & *Episyrphus balteatus*

FIGURES

(a)



(b)

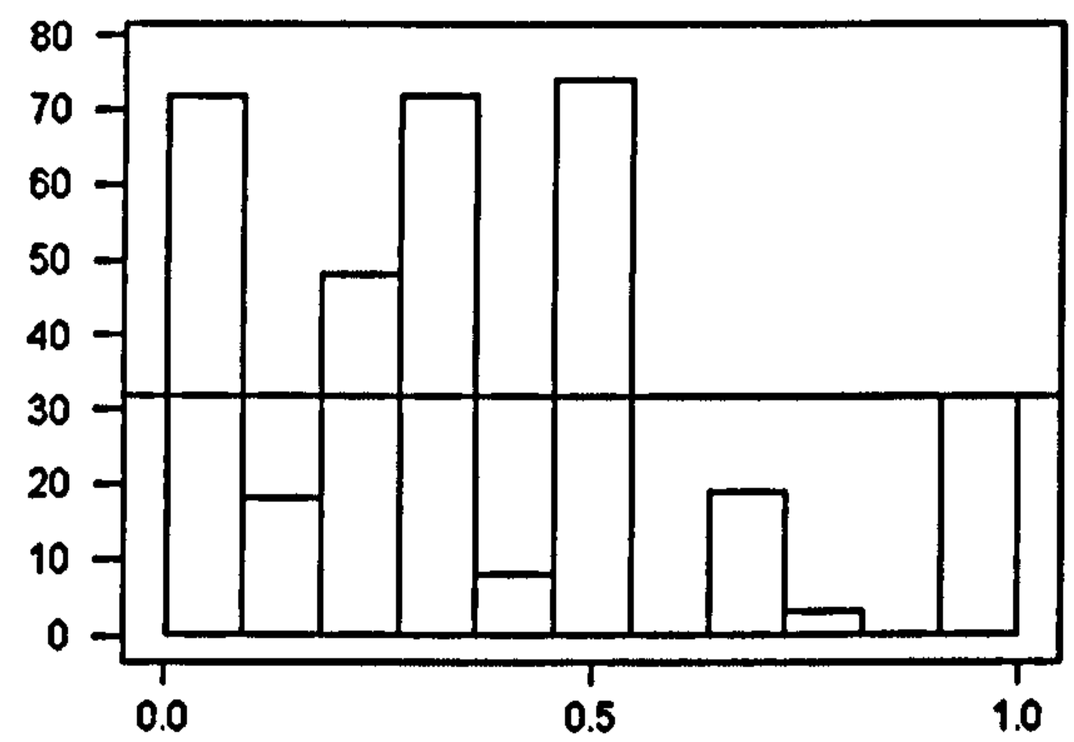
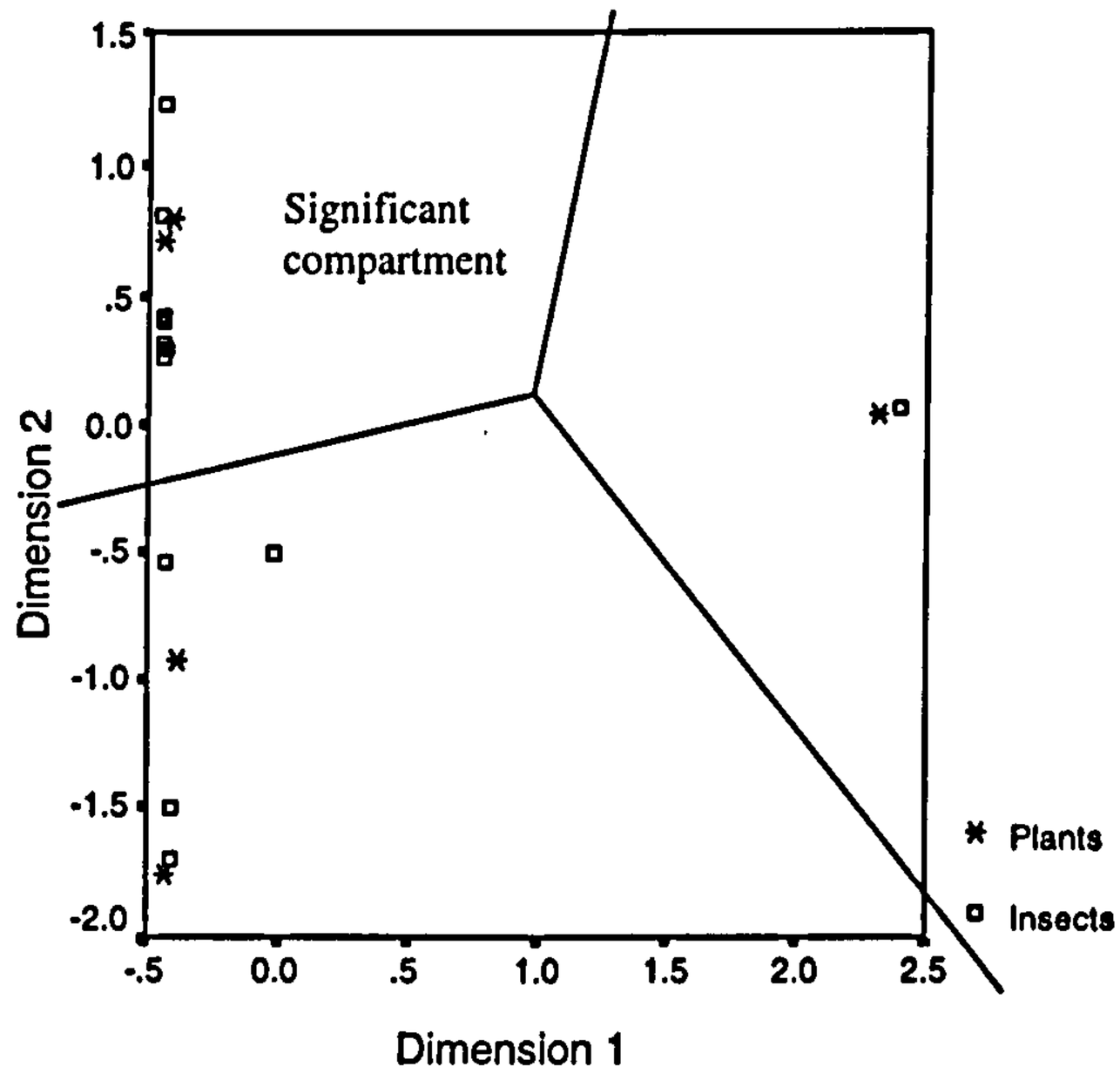


Figure 4.1 Example of the frequency distributions of Sij values in both the visitation (a) and pollen transport webs (b) of an old heathland, Arne Old.

(a)



(b)

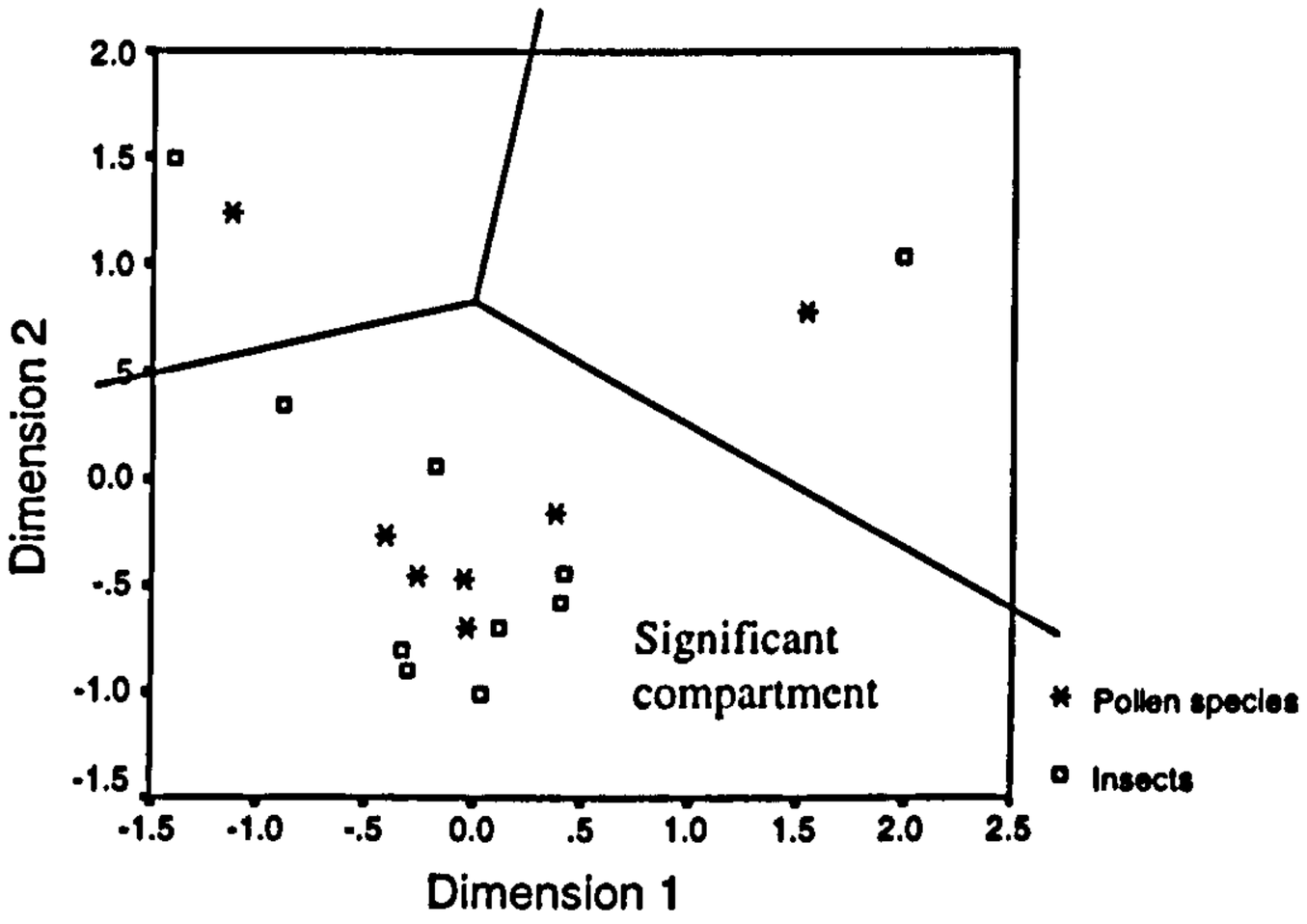


Figure 4.2 Two examples of ordinations from the correspondence analyses: a) visitation (insect perspective) for Hyde Old and b) pollen carriers (plant perspective) for Gore Old. In each case three potential compartments were identified (separated with lines), but only one was significant.

CHAPTER FIVE

Competition between honeybees and bumblebees

CHAPTER FIVE

Competition between honeybees and bumblebees

SUMMARY

While Apis mellifera *is known to be a strong competitor in many parts of the World, the species is rarely viewed in this light in its native range. However, since honeybees are sometimes kept at very high densities, they may displace competing insects through resource depletion. Here I present evidence of a negative association between honeybee and bumblebee abundance on old dry lowland heath in southern England. This negative association was not reflected in a decrease in bumblebee species diversity, nor was evidence found for a change in bumblebee foraging behaviour with increased honeybee abundance.*

5.1 INTRODUCTION

5.11 Competition by the honeybee

The European honeybee, *Apis mellifera* L., has been introduced to terrestrial ecosystems all over the world for the purposes of pollination and honey production (Michener 1974; Sugden and Pyke 1991), and the species is unique among insects in forming such a strong mutualism with humans. However, its spread has been detrimental to at least some native pollinators. For example, in New South Wales, Australia, Gross (2001) recorded fewer visits by native bees to the flowers of *Dillwynia juniperina* where honeybees where abundant, because the latter depleted the standing crop of nectar in the flowers. Similarly, Kato *et al.* (1999) found evidence of a decline in native bees following the introduction of honeybees to the Pacific Bonin Islands in the 1880s. This was augmented by the invasion of nectariferous weeds, which provided the honeybees with resources at the times of year when native flowers were limiting. In a final example, Schaffer *et al.* (1983) experimented with honeybees on *Agave schottii* in Arizona. They found that honeybees reduced the standing crop of nectar in an experimental plot to the detriment of both native bumblebees and solitary bees. Moreover, when apiaries were removed from the experimental plot, feral honeybees gradually claimed the place which had been occupied by the domesticated honeybees. Although the native bees initially responded positively to the removal of apiaries, their recovery was reversed as feral bees became more abundant.

In Europe, where the honeybee is native, it is usually assumed to be of little consequence to other pollinators, because these have evolved and maintained populations in its presence. For example, European bumblebees have evolved longer tongues than their American counterparts (Inouye 1977) and this allows them to forage on plant species not visited by the short-tongued honeybees (Williams 1986). Therefore, when concerns do arise over the effects of honeybees, they focus mainly on the need to provide a diverse array of floral resources for resource partitioning to take place (e.g. Comba *et al.* 1999).

The presence of apiaries means that vast amounts of floral rewards are harvested by single colonies of honeybees and this reduction in the resource base could lower the abundance of competing species. For example, Heinrich (1979) calculated that a single, strong apiary in the United States would in one year collect the equivalent amount of nectar and pollen to support 38,400 bumblebee reproductives, or 102 colonies. Furthermore, once

honeybees are established in an area, they could be more resilient to temporal changes in local resource availability, both because of their large potential foraging ranges (Visscher and Seeley 1982; Beekman and Ratnieks 2000) and because their food reserves, which are partly assured by the beekeeping management, can be utilized when the costs of foraging outweigh the benefits. Bumblebees do not have such a buffer but must instead rely on their ability to forage under sub-optimal conditions (Heinrich 1976; Corbet *et al.* 1993).

5.12 Bumblebees

In England populations of bumblebees (*Bombus* spp.) have decreased for at least 40 years while the number of species has declined from 19 to 16 (Williams 1982; Williams 1986, Benton 2000; Carvell 2002). This has mainly been brought about by changes in land use and loss of habitat resulting from agricultural intensification (Williams 1982; 1986). Given that bumblebee populations are now smaller and more fragmented than before, it is relevant to investigate how the remaining populations relate to both the physical and biotic aspects of their environment, including competition by honeybees.

5.13 Bee competition on old and restored heathlands

Honeybee competition could be particularly significant on heathlands, because the low number of plant species may limit the degree to which competitors can locate alternative forage. However, the quantitative heathland sampling in 2001 (Chapter 3) suggested a difference among old and restored heaths in the effect of honeybees upon bumblebee abundance: while old heathlands appeared to show a negative association between the abundance of honeybees and the abundance of bumblebees, such a pattern was not evident on restored heathlands (Figure 5.1). It is therefore possible that bumblebee establishment on restored heaths is not influenced by honeybee competition, but is limited by such factors as the availability of nesting sites and the temporal constancy of floral rewards on the heathlands and their surrounding habitat (Osborne *et al.* 1991; Edwards 1996; Carvell 2002). Therefore, the honeybees could in effect be filling a vacant niche on restored heathlands, and effect pollination which might otherwise not have taken place.

5.14 Aims

A study was carried out to investigate further the negative association between honeybees and bumblebees in the 2001 heathland data. This was done by sampling a higher number of

old heathlands. The aim was to determine if heathlands with high honeybee abundance had fewer bumblebees relative to heaths with low honeybee abundance. If this was confirmed, both the datasets from 2001 and 2002 would be explored for possible clues for evidence of competition between honeybees and bumblebees. Since we would expect to see an increase in resource partitioning with an increase in bee competition, similarity coefficients on the feeding behaviour should vary with the densities of bees and floral resources. Moreover, if honeybee competition is relevant on old heathlands but not on restored heathlands, we would expect similarity coefficients to differ between the two types of heathland in the 2001 data.

5.2 METHODS

5.21 Bee association 2002

In late July 2002 a study was carried out on 19 old heathlands in the Poole Basin, southern England (Figure 5.2). Sampling took place on dry, sunny days between 10 in the morning and 4 in the afternoon. In the centre of each heathland, a 100 m transect was laid out in a random, fixed direction, although paths, tall bushes and trees were avoided. The transect was sampled twice and all honeybees and bumblebees visiting flowers within one metre on either side of the transect line in front of the recorder were caught and identified, with a note of the flower species which they were visiting. Bumblebees were temporarily stunned with CO_2 to aid their identification, while honeybees were kept in individual vials until the end of the study when all were released. Only the specimens of bumblebee that were too difficult to identify in the field were killed with ethyl acetate and brought back to the laboratory for identification. Because of the difficulty in distinguishing workers of *Bombus lucorum* L. and *Bombus terrestris* L., these species were recorded as *Bombus lucorum/terrestris*, similar to Dicks *et al.* (2002).

After recording the number of flower-visiting bees, the abundance of each flower species was quantified. Where species were represented with only a few flower units, these were counted individually, otherwise floral abundance was estimated from random 1 m quadrats along the transect. Other recorded variables were the time of day and the ambient temperature.

5.22 Data analysis

The data were analysed by correlation and multiple regression (Sokal and Rohlf 1995). To reduce the risk of Type 1 errors in multiple correlations, the Bonferroni method was used to lower the alpha value of individual tests in order to get an overall alpha value of 0.05 for all correlations on the same variable (Sokal and Rohlf 1995). Multiple regression was used because it allows potentially interacting predictor variables to fit a model that may better account for the variation in the dependent variable than would any single variable. However, the analysis also requires a large number of observations that should exceed the number of predictor variables by at least 5:1, although a more acceptable ratio is about 10:1 (Kleinbaum *et al.* 1988). Consequently, only 2 regressors were used in any one analysis.

5.23 Bee foraging patterns

The Bray-Curtis coefficient, *Cz* (Bray and Curtis 1957), was used to compare the similarity of bee abundances and foraging patterns in both the 2001 and 2002 quantitative data. This coefficient is related to the Sørensen index of similarity (Sørensen 1948) but is better suited to quantitative data because of its sensitivity to sample size and because rare interactions are not given disproportional weight. The coefficient has the formula:

$$Cz = \frac{2w}{(a+b)} \qquad \textbf{Equation 5.1}$$

where, in the present study, w is the sum of the lowest number of interactions with plant species common to both honeybees and bumblebees, a is the sum of interactions with species visited by honeybees only and b is the sum of interactions with species visited by bumblebees only. A high *Cz* value means that honeybees and bumblebees forage on the same plant species, whereas a low value means that they mainly forage on different species or that the bee populations are very uneven. The coefficient was calculated for each site in the 2002 data. For the 2001 data, values were calculated for each sample taken from each site during the season, provided the sample contained both honeybees and bumblebees.

Bumblebees were considered first as a whole and second split into two groups of either short to medium-tongued or long-tongued bees according to Williams (1989) and Carvell (2002) This was done both because tongue length is important in determining on which flowers bumblebees can feed and because the abundance of individual bee species was sometimes too low to provide reliable estimates of the species' behaviour.

5.24 Rates of increase 2001

Rates of increase, *r*, were calculated to investigate the seasonal recruitment in the populations of honeybees and short-tongued bumblebees on the 8 heathlands in the 2001 data. The rate was calculated from the equation:

$$r = \frac{ln(N_t) - ln(N_0)}{t} \qquad \textbf{Equation 5.2}$$

where N_0 is the population at time *0* and N_t is the population at time *t*. If honeybees have a negative effect on bumblebees, we would expect bumblebee recruitment to be reduced on heathlands with many honeybees.

5.3 RESULTS

5.31 Bee association 2002

Honeybees and bumblebees were present on all 19 sites. Honeybee abundance varied from 4 to 81 bees per transect (mean = 30.89, median = 23), while bumblebees varied from 2 to 17 individuals per transect (mean = 8.26, median = 7), belonging to between 1 and 5 species (mean = 2.42, median = 2). Appendix C5 lists the bee species and their relative abundance. The relative abundance of the bumblebee species was very uneven, with the short-tongued *Bombus jonellus*, *Bombus lapidarius* and *B. lucorum/terrestris* being the most abundant and widespread species, while the long-tongued species *Bombus humilis* and *Bombus pascuorum* were least abundant and widespread.

Figure 5.3 is a diagram of the total bee abundance on the 19 heathlands. The relationship between honeybees and bumblebees was best described as negatively exponential (r^2 = 34.5%, p = 0.008); consequently the data were log-transformed prior to stepwise multiple regression. With bumblebee abundance as the dependent and honeybee abundance and flower abundance as regressors, the model had a fair fit (r^2_{adj} = 29.4%) although honeybee abundance was the only significant predictor ($F_{1,17}$ = 8.512, p = 0.01). Thus bumblebee abundance significantly decreased with an increase in honeybees. Repeating the analysis for only short-tongued species resulted in a model of a marginally better fit (r^2_{adj} = 30%) with honeybee abundance still being the only significant predictor ($F_{1,17}$ = 8.73, p = 0.009). Neither honeybee abundance nor bumblebee abundance correlated with flower abundance at the time of sampling (honeybees: Pearson's r = -0.339, p = 0.155; bumblebees: Pearson's r = 0.238, p = 0.326).

The number of *Bombus* species was regressed against both honeybee abundance and flower abundance. This resulted in a model of fair fit (r^2_{adj} = 37.5%) but here the only significant predictor was flower abundance ($F_{1,17}$ = 11.8, p = 0.003). Stepwise multiple regression of *Bombus* species against bumblebee abundance and flower abundance also gave a model of fair fit (r^2_{adj} = 47.5%) and the overall relationship was significant ($F_{2,16}$ = 9.14, p = 0.002), although flower abundance was again the only significant predictor (beta = 0.45, p = 0.034) while bumblebee abundance was a statistically weak predictor (beta = 0.4, p = 0.056).

Bumblebee abundance was neither correlated with the time of sampling nor with the ambient temperature (time of sampling: Spearman's rho = 0.17, p = 0.484; ambient temperature: Spearman's rho = 0.004, p = 0.988). This was similar for the number of *Bombus* species (time of sampling: Spearman's rho = 0.20, p = 0.404; ambient temperature: Spearman's rho = -0.19, p = 0.449). Nor was honeybee abundance correlated with any of these factors (time of sampling: Spearman's rho = -0.16, p = 0.524; ambient temperature: Spearman's rho = -0.15, p = 0.538). Thus when sampling only between 10 a.m. and 4 p.m. time and temperature were rendered insignificant.

5.32 Bray-Curtis coefficients for the 2002 data

Figure 5.4 is a plot of Bray-Curtis coefficients against bee abundance on the 19 old heathlands. The coefficient was negatively associated with honeybee abundance and positively associated with bumblebee abundance (honeybees: Spearman's Rho = -0.636, p = 0.003; bumblebees: Spearman's Rho = 0.647, p = 0.003. With the Bonferroni correction method, this section's correlations with Bray-Curtis coefficients must each be more significant than 0.0102 for an overall alpha value of 0.05). Therefore, where honeybees were most abundant, bumblebees were fewer and/or foraged on different flower species. A stepwise multiple regression with honeybee abundance and bumblebee abundance as regressors gave a model of fair fit ($r^2_{adj} = 42.2\%$) but also showed that honeybee abundance was the only significant predictor ($F_{1,17} = 14.15$, $p = 0.002$). Bray-Curtis coefficients were not associated with total flower abundance, the abundance of individual flower species or with the number of flower species present at the time of sampling.

5.33 Bray-Curtis coefficients for the 2001 data

There was a significant change in Bray-Curtis coefficients over the 2001 season on both old and restored heathlands and both when considering bumblebees as a whole and when considering only the short-tongued bumblebees (repeated measures anova; all bumblebees: $F_{4,24} = 7.289$, $p = 0.001$; short-tongued bumblebees: $F_{4,24} = 8.021$, $p < 0.001$). This change in foraging similarity over the season reflects both the change in flower resources and the change in bee numbers. In contrast, there was no significant difference between the old and restored heaths (repeated measures anova; all bumblebees: $F_{4,24} = 0.098$, $p = 0.982$; short-tongued bumblebees: $F_{4,24} = 0.344$, $p = 0.846$). When ranking the coefficients, the old and the restored heaths within each pair were perfectly associated, both for short-tongued and

long-tongued bumblebees, which means that sharing patterns were similar on the old and the restored heathland within each pair.

In neither the old nor the restored heathlands were Bray-Curtis coefficients, based on all bumblebees or the short-tongued bumblebees only, correlated with honeybee abundance. This is shown in Figure 5.5 and Figure 5.6 where, for clarity, the mean values are shown for old and restored heathlands, respectively. Therefore, there is no evidence of a change in the foraging patterns of short-tongued bumblebees as honeybees increase. For the old heathlands, this contrasts with the 2002 data.

Long-tongued bumblebees were too few on individual sampling dates to allow for a similar analysis, but when the abundance of these bees was summed for the entire season, the four old heathlands showed a perfect, negative association between Bray-Curtis coefficients and honeybee abundance. In contrast, there was no apparent association between Bray-Curtis coefficients and honeybees on the restored heathlands.

5.34 Bees and flower abundance in the 2001 data

On both old and restored heathlands, honeybees were correlated with flower abundance on individual sampling dates (old heathlands: Spearman's Rho = 0.596, p = 0.006; restored heathlands: Spearman's Rho = 0.647, p = 0.002) (for flower abundance see Chapter 3; Figure 3.8). There was weak evidence of this also being the case for short-tongued bumblebees on old heathlands, but with the Bonferroni correction, the result of Spearman's Rho = 0.493, p = 0.027 for short-tongued bumblebees was not significant. No association existed on restored heathlands (Spearman's Rho = 0.184, p = 0.439).

5.35 Rates of increase in 2001

Figure 5.7 is a plot of the rates of increase in honeybees and short-tongued bumblebees over the season for the 8 heathlands sampled in 2001. These graphs show only four values for the season, because short-tongued bumblebees and honeybees were not present on all heathlands until the fourth sampling date, which was in early July. On both the old and the restored heathlands, honeybees increased until mid August after which the rates of increase were negative. Short-tongued bumblebees increased at first, then decreased between late July and mid August. There was a then modest increase until early September after which the rates of increase went negative again. Long-tongued bumblebees were too few to permit a similar analysis.

On individual old heathlands, the rate of increase for short-tongued bumblebees was correlated neither with the rate of honeybee increase nor with honeybee abundance (honeybee rate of increase: Spearman's Rho = 0.112, p = 0.68; honeybee abundance: Spearman's Rho = 0.144, p = 0.594). However, on restored heathlands, the rate was positively correlated with the honeybee rate of increase (Spearman's Rho = 0.735, p = 0.001) but with the Bonferroni correction, the result of Spearman's Rho = 0.51, p = 0.044 was not significant for honeybee abundance.

5.4 DISCUSSION

While there was a clear negative association between the abundance of honeybees and bumblebees, there was insufficient evidence to support the hypothesis that honeybee competition is the cause of this association. In this section I first review the findings. Then I discuss the implications of these findings in the light of alternative explanations. Finally, I comment on the implications for future studies into the effect of honeybees on wild bees.

5.41 The negative association

The 2002 data suggested that bumblebees were negatively associated with honeybees. This could indicate that competition brought about by high densities of honeybees had had an adverse effect on bumblebees. However, in the analysis honeybees only explained 29.4% of the variation in bumblebee abundance in 2002 and this suggests than any effect of honeybees is only one of a number of potential factors influencing bumblebee abundance. The analysis also showed that bumblebee species richness was unaffected by honeybees. This means that if honeybees do cause a reduction in competing bumblebees when they are abundant, this does not appear to affect bumblebee species diversity.

5.42 Coefficients

Since the Bray-Curtis coefficient takes both abundance and foraging patterns into account, a negative effect of honeybees will cause a reduction in this index if bumblebees either starve, find alternative flower species to feed on or forage at a different locality with less competition. Indeed, the coefficient was negatively associated with honeybees on the 19 old heathlands (Figure 5.3). Moreover, in the 2001 data it also appeared to be associated with the site pairings and therefore the general area in which pairs were located. This is similar to other results in the 2001 data, where locality had an effect on the species diversity in both the old and the restored heaths within pairs (Chapter 3).

However, the Bray-Curtis coefficient alone is not evidence of competition. For example, if bumblebees were declining in response to other factors than honeybees, which could in effect just be filling an empty niche, this would also lead to smaller Bray-Curtis coefficients. Even so, it is interesting that short-tongued bumblebees and their associated Bray-Curtis values decreased in August while flowers and honeybees were still increasing.

While the Bray-Curtis coefficient for short-tongued bumblebees did not appear to be affected by honeybees on the 4 old heathlands in the 2001 study, a negative association

existed for the coefficient based on the long-tongued bumblebees for the entire season. Because of the low abundance of these bees, the data do not allow this to be proven. However, if the effect is real, it suggests that long-tongued bumblebees are more likely to be affected by honeybee competition than are short-tongued bumblebees, perhaps because the heathlands do not provide many plant species on which the honeybees cannot feed. Moreover, the long-tongued bumblebees could also suffer from competition by other bumblebees. For example, the most abundant bumblebee species was the short-tongued *Bombus lucorum/terrestris*. In Tasmania, the recently introduced *B. terrestris* has proved to be a strong competitor in the local pollination system (Hingston and McQuillan 1998; Stout and Goulson 2000) and it could behave in a similar manner in these British heathlands.

The main blow to the honeybee competition hypothesis came from the 2001 rates of bumblebee increase, which, on the old heathlands, showed no evidence of being affected by honeybee density. Furthermore, there was a positive association between bumblebee increase and honeybee increase on the restored heathlands, although this could just indicate that populations of bumblebees on restored heathlands respond more to the heathland restoration than they do to honeybee competition. While this therefore cannot support the competition hypothesis, it is not evidence of the opposite either. For example, it is possible that the negative association between honeybees and bumblebees in the 2002 data is the result of past competition and that the bumblebee populations on these heathlands are currently stable.

5.43 Flower abundance

In general, we expect bees to compete when flower rewards are limiting. Therefore, the lack of associations with flower abundance in the 2002 study suggests that competition is unlikely, as the resource does not appear to be limiting. However, Zimmerman and Pleasants (1982) questioned whether flower counts are good measures of the nectar resources available to pollinators, since some flowers may have been emptied of their rewards and not all flowers offer rewards as soon as they open. In response, Tepedino and Stanton (1982) argued that the true measure of resource availability is almost impossible to obtain, and that since bees can collect both nectar and pollen, their response to resource availability will differ over time. They suggested that an improved method could be to weigh flower abundance by the average size of the flowers. I attempted this correction on the 2002 data but since it did not change the result it has not been reported here.

In contrast, honeybees correlated with flower abundance in the 2001 data. The bumblebees did not show a similar association, but this could reflect a main difference in these social bees: honeybees can communicate to each other where to find the most profitable patches in the landscape (Visscher and Seeley 1982), but bumblebees cannot do this; the only social influence on bumblebee foraging is that individuals forage in response to changes in the colony's nectar store (Inouye 1978).

The lack of association with flowers in the 2002 data could reflect that bees in late July have more than enough flower resources available for their needs, and that foraging on one heathland site over the next makes little difference. This suggests that any effect of honeybees on bumblebees should be strongest when resources are limiting, such as before the flowering of the ericaceous shrubs. Therefore in a future study, the heathlands should be sampled at other times of the year also.

5.44 Other factors determining bumblebee abundance

Many factors must interact to influence how many bumblebees can be found on heathlands. Notable among these are the availability of nesting and hibernation sites, 'patrolling' sites for male bees and flower constancy (Corbet 1992; Edwards 1996; Cane 2001). However, by sampling only old, dry lowland heath, the availability of the former were controlled for, with such components as the amount of moss, lichen and litter, the presence of abandoned mammal nests, the amount of exposed ground, vegetation structure, etc. assumed to be similar across the sites. The 2001 heathland sampling started in April and showed a steady increase in flower abundance on old heathlands up until the peak flowering of *Calluna vulgaris*. However, no data were collected before April, nor was the habitat surrounding the heathlands sampled for floral resources. Approximately 35 km separated the two most distant study sites in 2002, but each heathland was within 1 and 4 km from other study sites. Therefore, bees from more than one heathland could be visiting localities with optimal forage in spring (Saville *et al.* 1997) and this may possibly make bumblebees less dependent on the *in situ* flower constancy over the season. The fact that locality influenced the Bray-Curtis values for paired sites may mean that bees on these sites forage on the same floral sources in spring.

Apart from resource depletion, other factors could influence a negative association between bumblebees and honeybees. For example, honeybees could pass on pathogens. Some pathogens are known to affect both honeybees and bumblebees (Macfarlane *et al.*

1995; Alford 1975), but they would be unlikely to give the honeybees any competitive advantage. All Dorset apiaries are currently affected by the mite *Varroa jacobsoni* Oudemans (R. Hogben, *pers. comm.*), but this species does not attack bumblebees. However, bumblebees are host to a wide range of parasites (Prys-Jones and Corbet 1991). It is possible that these can stress their hosts and make them more susceptible to deteriorations in their environment, including increased exploitative competition.

5.45 Future directions

Despite the apparent negative association between honeybees and bumblebees, no conclusive evidence was found of a causal effect. In order to improve this study, future sampling should be carried out with regard to the foraging patterns of these bees throughout the season, e.g. where do bees feed in early spring? To what extent do bumblebees feed in other habitats and how far away? Finally, since honeybee competition may be most significant for the long-tongued bumblebees, these species deserve special attention. I hope that the present study will also be followed up by studies on other habitat and in other geographical regions. If a negative relationship turns out to be representative of the general situation, more detailed studies should be carried out to develop guidelines for how many apiaries a given habitat can support without it being detrimental to local bumblebee populations. Moreover, if bumblebee populations continue to decline in the United Kingdom, a part of their recovery could involve habitat improvement through local reductions in honeybee numbers.

In both the United Kingdom and North America, the honeybee is now less abundant (Allen-Wardell *et al.* 1998). This change has been caused by a combination of infestation with varroa and tracheal mites, as well as declining financial incentives to keep bees primarily caused by competition from cheap imported honey (Watanabe 1994). However, because of fears of a pending pollination crisis, *A. mellifera* is sometimes promoted as the suitable agent fill vacant niches (Carreck and Williams 1998). If evidence is found that honeybees make the situation worse for bumblebees, the solution may not be to fill empty niches with honeybees but to conserve and restore the diversity of wild bees.

FIGURES

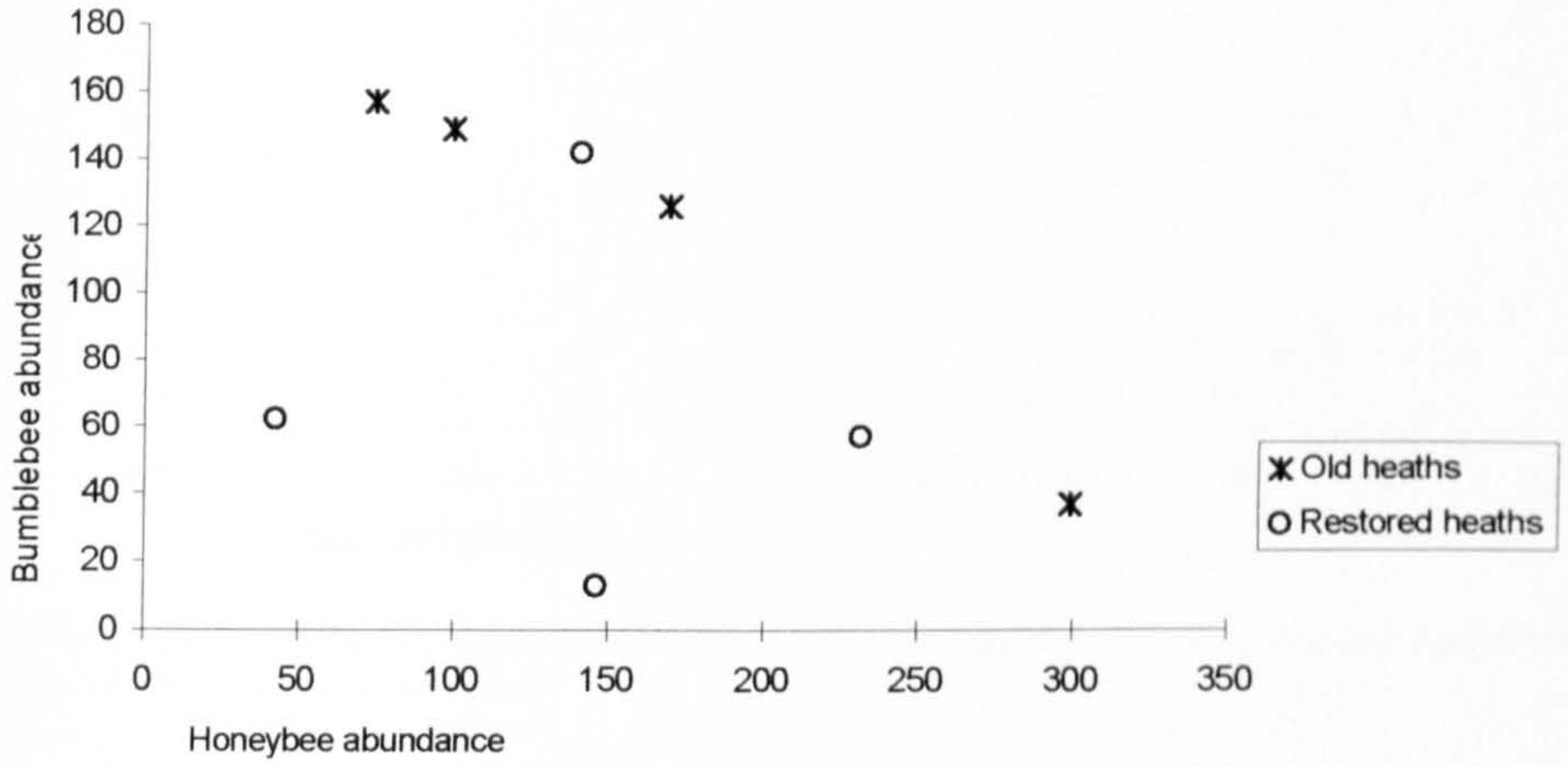


Figure 5.1 Honeybees and bumblebees on old and restored heathlands in the Poole Basin, Dorset (total for fieldwork April-September 2001).

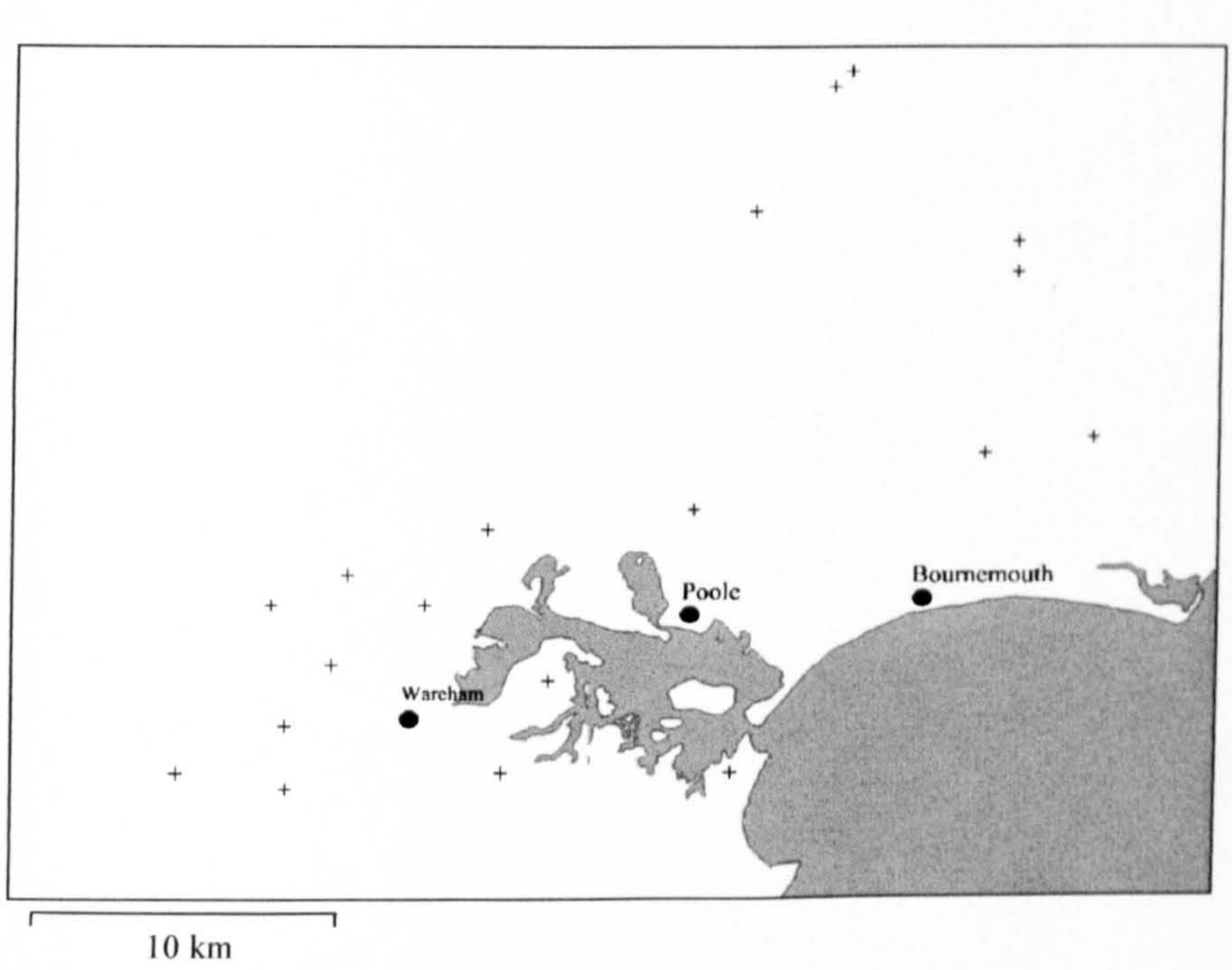


Figure 5.2 A map of the Poole Basin, South England. 19 old heathlands (marked with crosses) around Poole Harbour were sampled in July 2002. Please consult Figure 3.1 for the regional context of the Poole Basin.

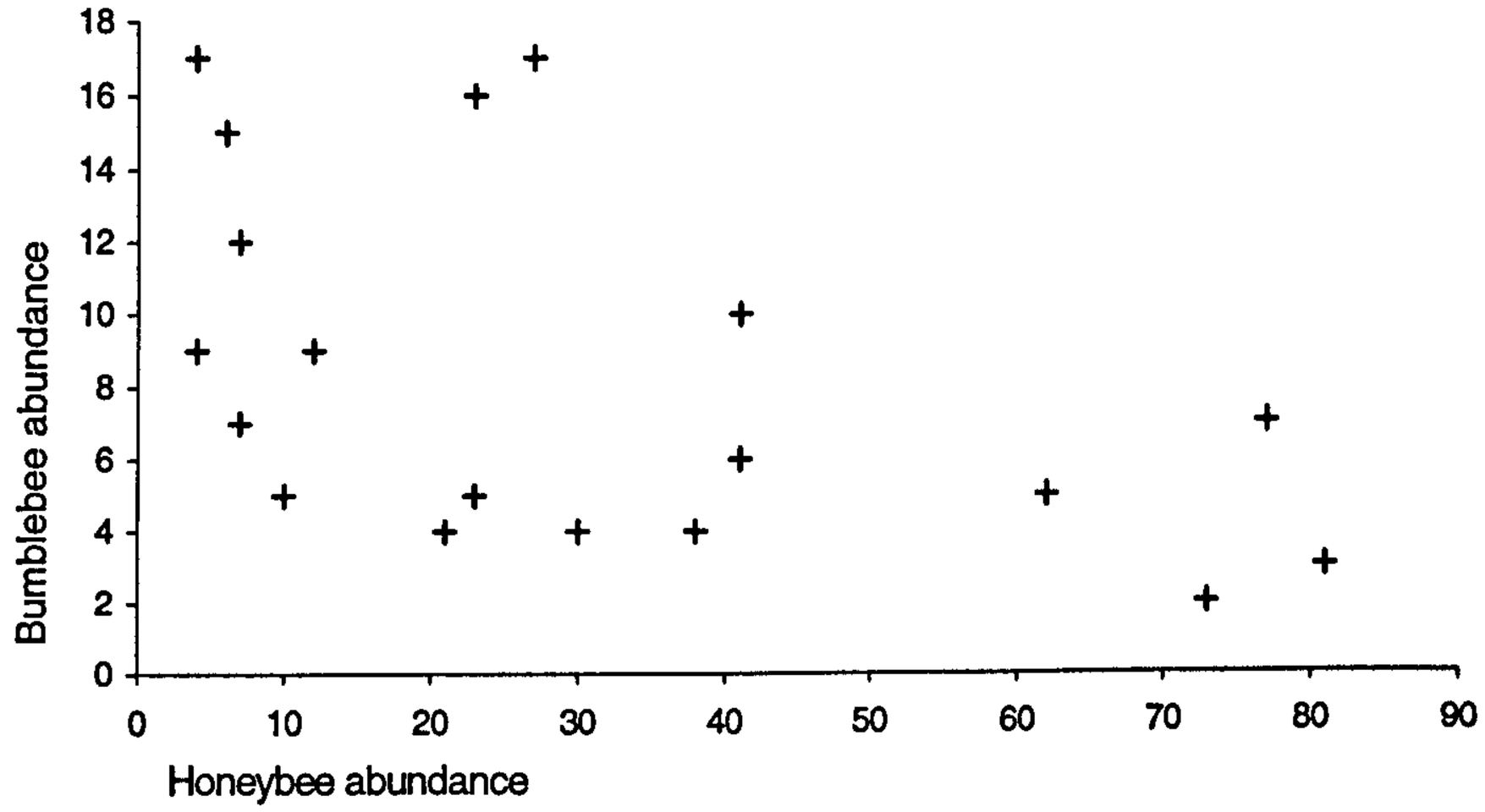
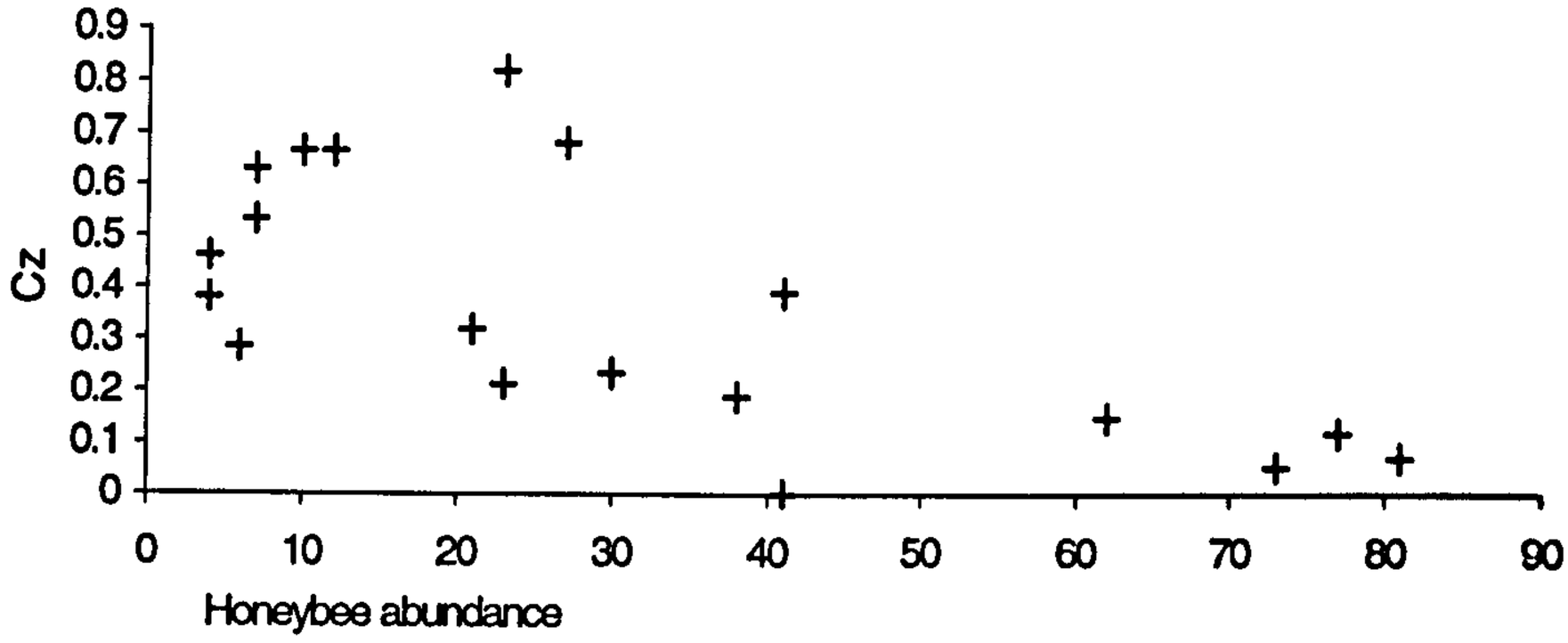


Figure 5.3 Plot showing a modest, negative association between bumblebee abundance and honeybee abundance on 19 old, dry lowland heaths.

(a)



(b)

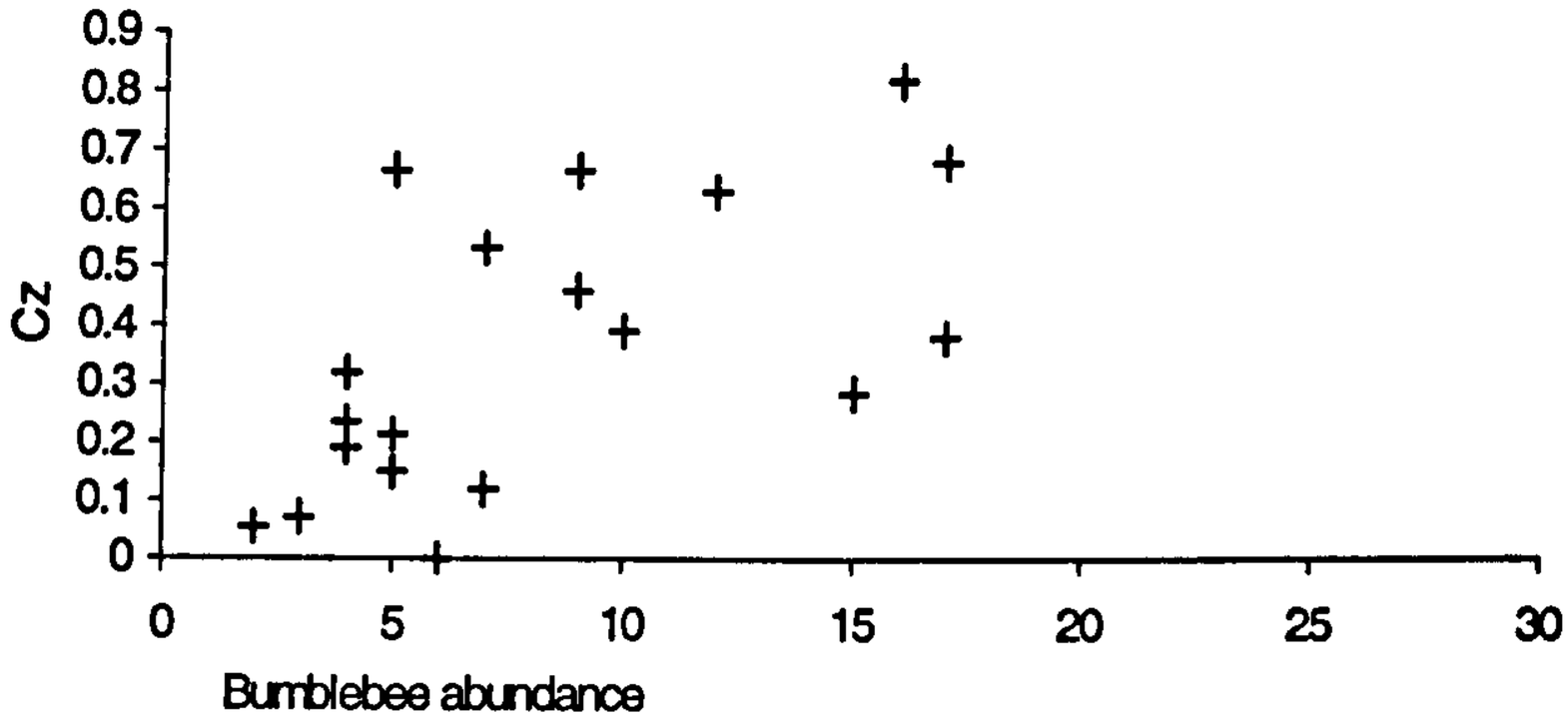


Figure 5.4 Bray-Curtis coefficients from 19 old lowland heaths plotted against honeybee and bumblebee abundance, respectively. Notice the different scales. (a) honeybees, (b) bumblebees.

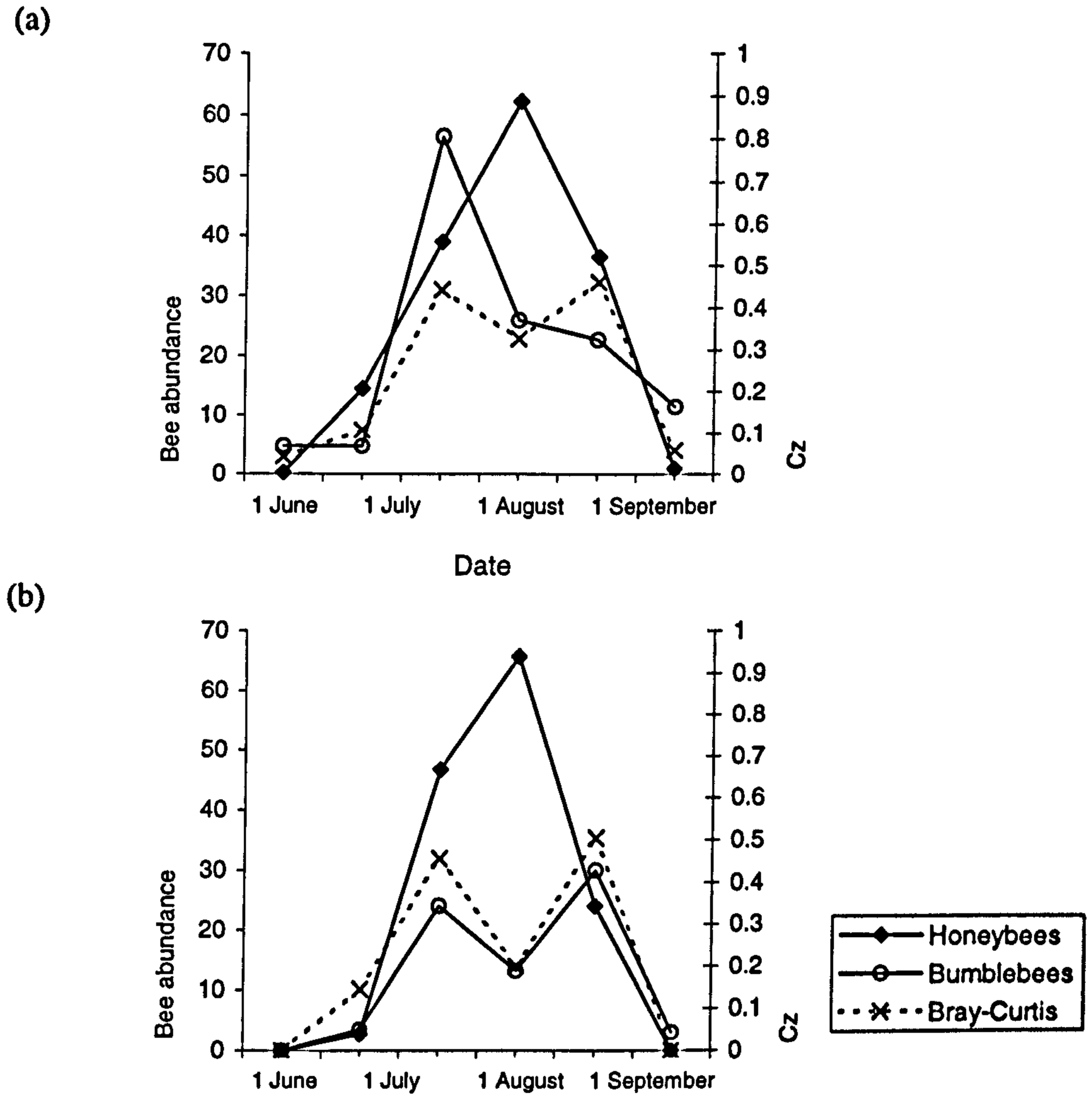
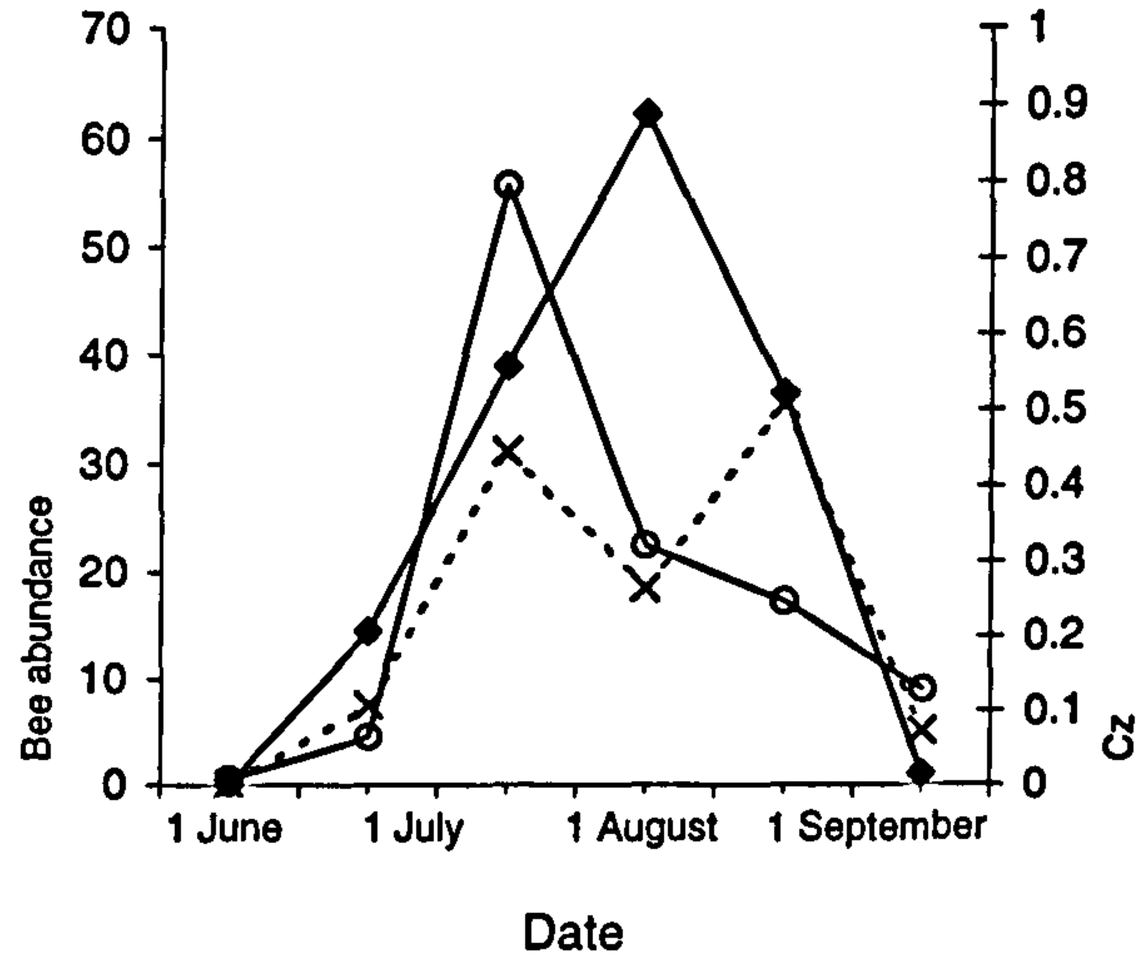


Figure 5.5 Plot of bee abundance and mean Bray-Curtis coefficients based on the total bumblebee data in 2001. (a) old heathlands, (b) restored heathlands.

(a)



(b)

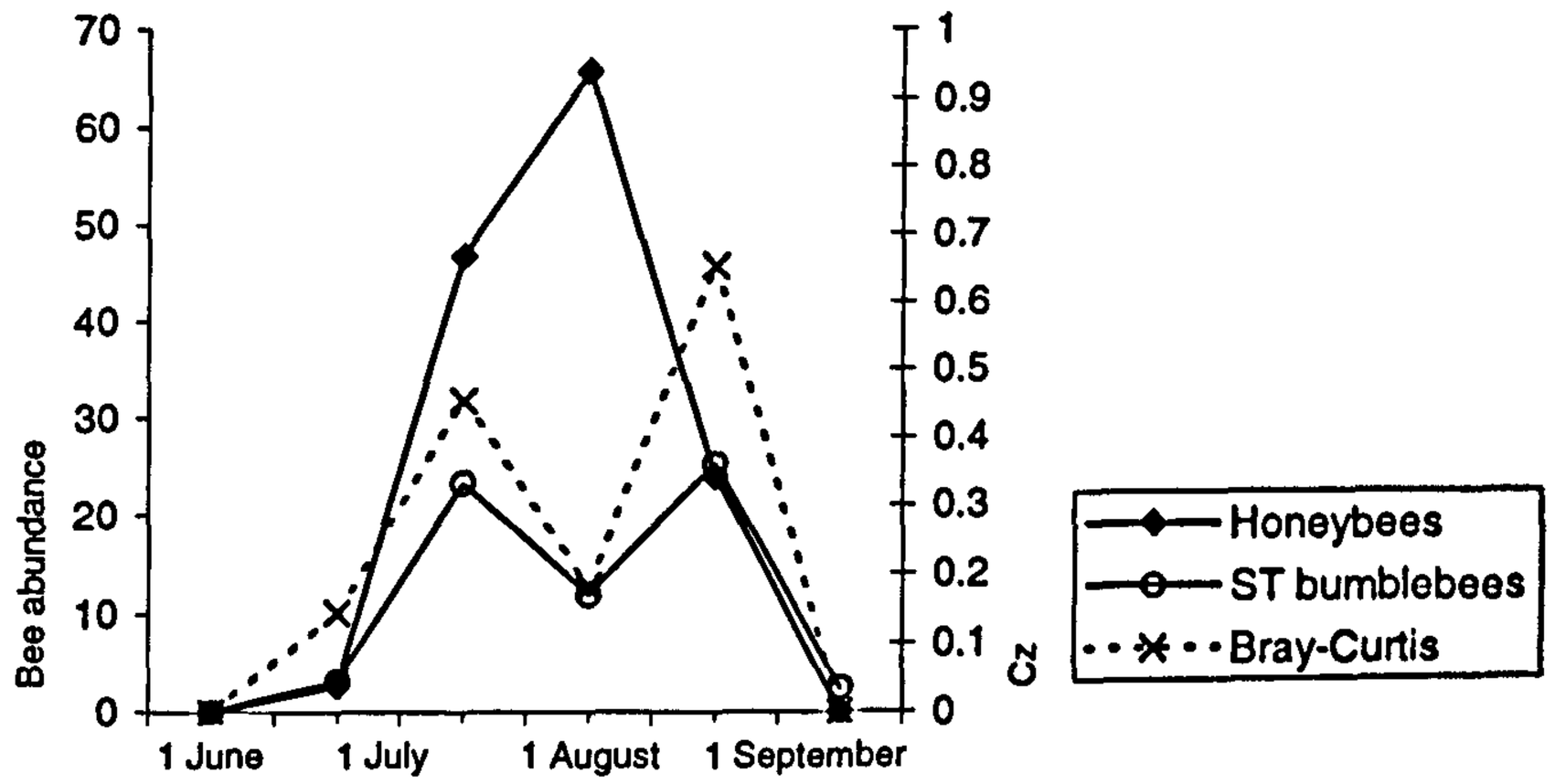
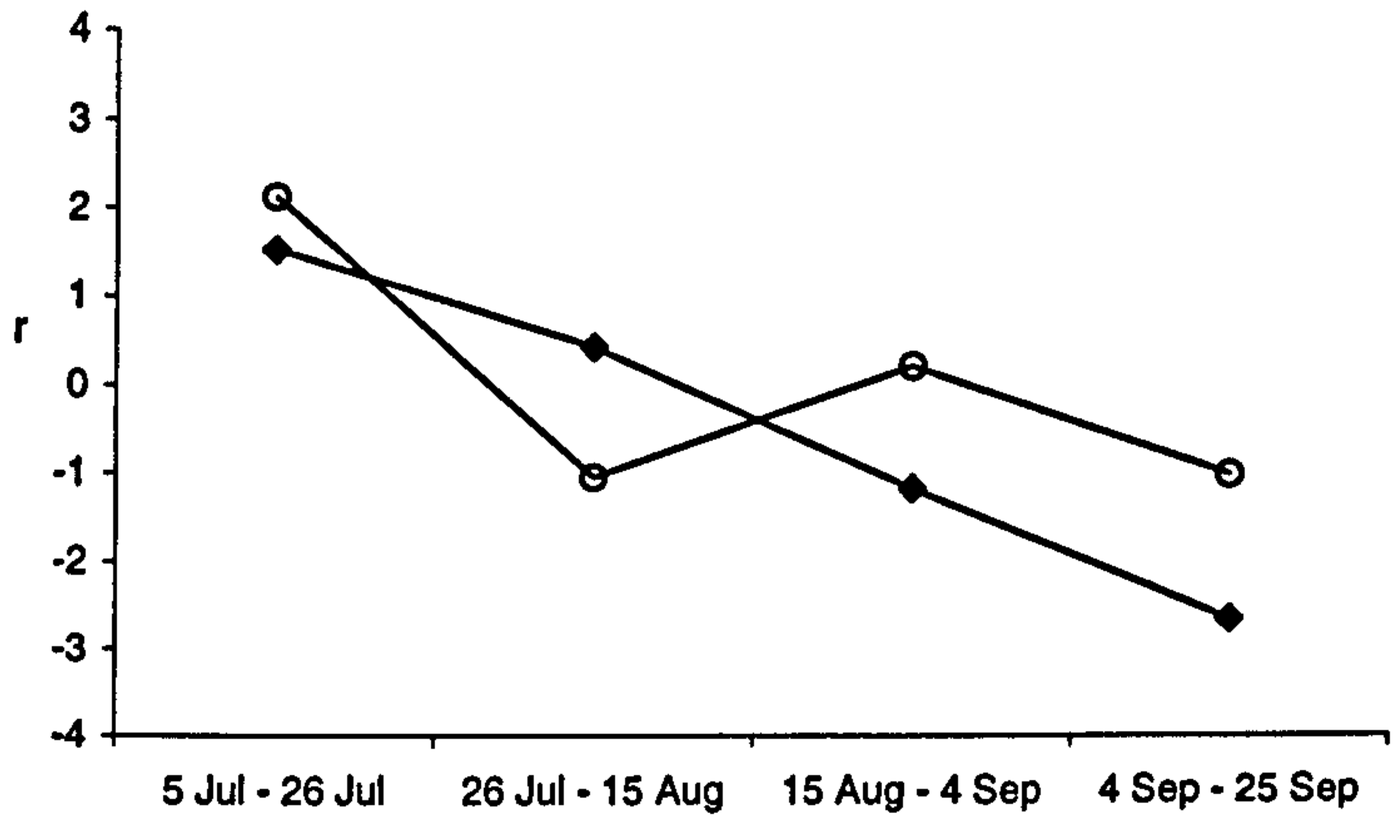


Figure 5.6 Plot of bee abundance and mean Bray-Curtis coefficients based on the short-tongued (ST) bumblebee data in 2001. (a) old heathlands, (b) restored heathlands.

(a)



(b)

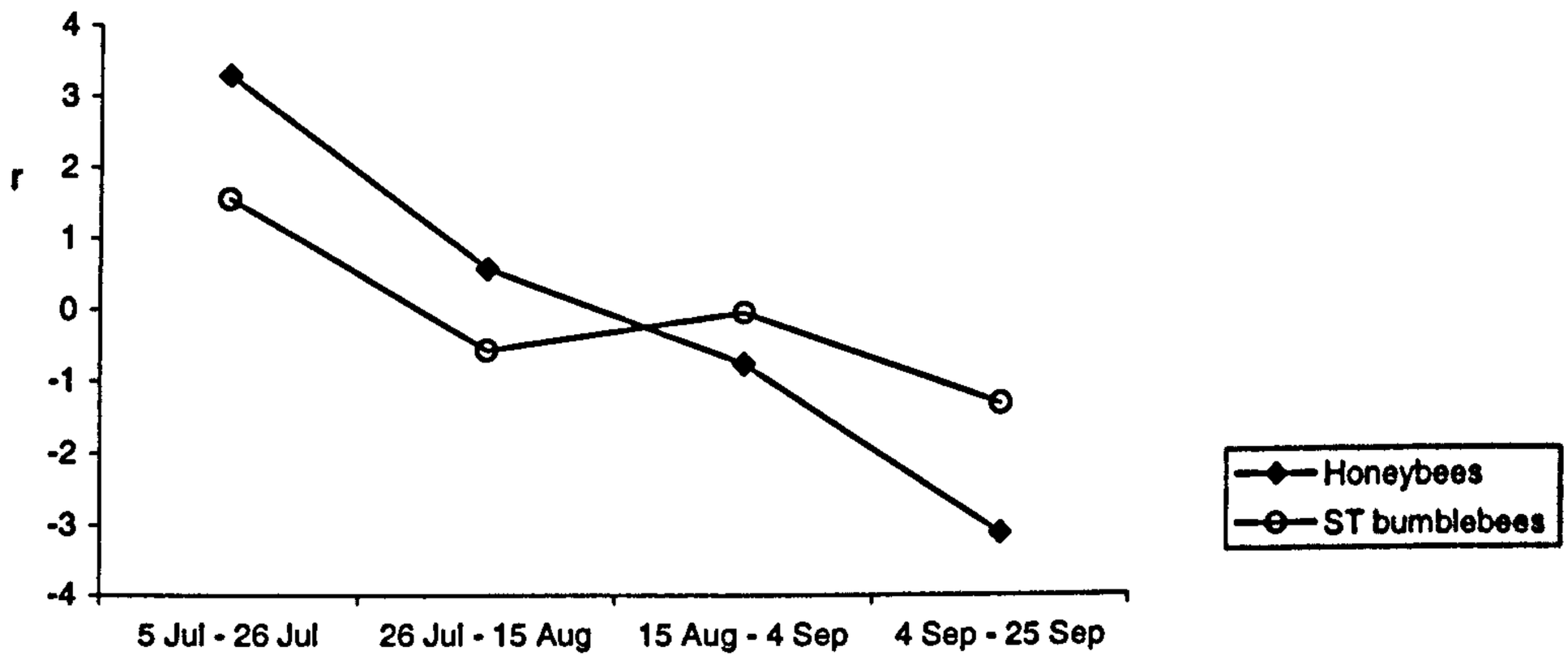


Figure 5.7 Plots of rates of increase in honeybees and short-tongued (ST) bumblebees between the five sampling dates in the 2001 data when both honeybees and bumblebees were found on all the 8 heathlands. (a) old heathlands, (b) restored heathlands.

CHAPTER SIX

Thrips pollination on heathland

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Thrips pollination on heathland

SUMMARY

Thrips are usually ignored in pollination studies, probably because they are very small, sometimes live inside flowers and are difficult to identify in comparison to e.g. bumblebees, butterflies or hoverflies. Yet thrips can be important pollinators. In 2001 the abundance of thrips was investigated in 4 pairs of old and restored lowland heath. In 2002 the seed set due to thrips pollination in Calluna vulgaris, Erica cinerea *and* Erica tetralix *was investigated on a restored heathland by excluding other insects from the flowers. Thrips were abundant on both old and restored heathlands. Moreover, they caused considerable seed set and were responsible for almost half the seed set in* C. vulgaris *and one third of the seed set in* E. cinerea *and* E. tetralix. *Although it is possible that this number was inflated by wind pollination, the wind alone could not account for all the seeds produced. Consequently, thrips pollination is concluded to be significant on these heathlands.*

6.1 INTRODUCTION

6.11 Thrips as pollinators

Thrips constitute an ancient order of small insects, Thysanoptera, whose species have evolved many types of feeding relationships, ranging from gall induction over ectoparasitism to pollination associations (Mound 2002). Because the order is ancient, thrips may have been some of the first pollinators. For example, while insect pollination is commonly thought to have evolved in concert with the rise of angiosperms in the Lower Cretaceous, about 135 million years ago, the fact that thrips today form intricate pollinator relationships with cycads has led some workers to speculate that these mutualistic interactions could have evolved in the Triassic, over 200 million years ago, long before the advent of angiosperms (Schneider *et al.* 2002). Furthermore, in some cases thrips and flower evolution has been very closely matched (Ananthakrishnan 1993).

Flower thrips live most of their lives on or inside flowers. They can be important pollinators and are sometimes the only known pollinators of certain plant species (Norton 1984; Annadurai and Velayudhan 1986; Velayudhan and Annadurai 1986; Baker and Cruden 1991; Ananthakrishnan 1993; Gurusubramanian and Ananthakrishnan 1994; Howard *et al.* 1995; Williams *et al.* 2001; Mound 2002; Schneider *et al.* 2002). For example, species of thrips were the only insects associated with the West Indies mahogany, *Swietenia mahagoni*, in Florida (Howard *et al.* 1995). Williams *et al.* (2001) working in New South Wales, found that one species, *Thrips setipennis*, was the sole pollinator of a shrub, *Wilkiea huegeliana*, at high altitude, while *T. setipennis* itself was widespread and found on 13 rainforest species.

Perhaps the small size of thrips is the reason why many pollination studies fail to consider the potential role of thrips, although authors sometimes point out this bias themselves (e.g. Kwak 1979; Costa *et al.* 1993; Reed 1995; Memmott 1999; Dicks *et al.* 2002). Moreover, in the quantitative flower visitation data (Chapter 3), thrips were recorded with only few individuals, although I realised that this was likely to be a gross underestimate of their true abundance.

6.12 Thrips on heathlands

Thrips are found in the flowers of *Calluna vulgaris*, *Erica cinerea* and *Erica tetralix* and are known to pollinate *Calluna* and *E. tetralix* (Hagerup 1950; Hagerup and Hagerup 1953). In *Calluna*, the heather thrips, *Ceratothrips ericae* Haliday (called *Taeniothrips ericae* in papers by Hagerup (1950) and Hagerup and Hagerup (1953)), deposits its ova in the swollen base of the corolla. Developing thrips can feed on both the pollen and the nectar-rich tissue inside the flower, which also provides a shelter from rain and wind. When they mature, the winged females climb up the stigma and take off in search of males, which are wingless and more rare (Hagerup 1950). In so doing, the female can affect self-pollination in her home flower, but she also carries pollen on her surface that can potentially fertilize flowers elsewhere. For *E. tetralix*, Hagerup and Hagerup (1953) documented that this species is used and pollinated by both *C. ericae* and *Frankliniella intonsa* Trybom. Nevertheless, the abundance and significance of thrips on heathlands is rarely investigated. In one study, Mahy *et al.* (1998) performed exclusion experiments on *Calluna* and concluded that wind pollination was common for this plant species. However, the method used by these authors would also allow thrips, if present, to effect at least part of the pollination, which the authors ascribed to the wind.

6.13 Aims

The aims of this study were two fold: First, to investigate the abundance of thrips in *Calluna vulgaris*, *Erica cinerea* and *Erica tetralix* in the 4 pairs of dry lowland heath that were sampled in Chapter 3, asking the question: has thrips abundance been reinstated in the 10 years following restoration? Second, to investigate the seed set caused by thrips on heathlands, here asking the question: what is the relative importance of thrips in the seed production of these plant species?

6.2 METHODS

6.21 Study 1: the abundance of thrips

This study was carried out simultaneously with the quantitative sampling on the 4 pairs of old and restored heathlands in 2001 (Chapter 3). In each transect, 5 random flowering stems of each of *Calluna vulgaris* and *Erica cinerea*, and 5 random umbels of *Erica tetralix* were collected at the 15 m, 30 m, 45 m, 60 m and 75 m marks or as close to these as possible. Each flower head was placed in a paper bag, marked with an ID number and immediately transferred to a killing jar, whereby the majority of thrips were killed inside their host flower. In the laboratory, individual flowers were examined under the dissecting microscope. The number of thrips found inside each flower was recorded and an average calculated per flower. Due to time constraints, no attempt was made to identify the thrips to species. Thrips identification can take a long time, partly because of their abundance and partly because each specimen has to be mounted on a microscope slide. However, for the purposes of this study, all flower-inhabiting thrips were assumed to behave in a functionally similar way.

Where the data conformed to the assumptions of parametric tests, repeated measures analysis of variance was used to compare the thrips numbers over the season (Sokal and Rohlf 1995). Where the data were not normal and homoscedastic even after transformation, the non-parametric Mann-Whitney U and Kruskal-Wallis tests were employed instead (Sokal and Rohlf 1995).

6.22 Study 2: thrips pollination on a restored heathland

This study was carried out on the restored heathland Holton Lee from mid-July to mid-September 2002. Here flowers were bagged to determine what proportion of the seed set in *Calluna vulgaris*, *Erica cinerea* and *Erica tetralix* could be ascribed to thrips.

Three treatments were applied to flowering stems on which flowers were about to open but none had done so yet: in Treatment 1, the flowering stem was treated with a contact insecticide (active agent: tetramethrin 0.31% w/w d-phenothrin 0.08% w/w; Johnson Wax Ltd.) to kill thrips present on the leaves, branches and immature flowers, before the stem was bagged in plastic perforated with 0.04 mm holes to prevent colonization by thrips from elsewhere. This purpose of this was to determine the proportion of seeds that was caused by

self-pollination with no external pollen vector. In Treatment 2, flowering stems were bagged with nylon netting of a 1 mm^2 mesh size. This allowed movement by thrips in and out of the bags but prevented larger insects, such as bees, butterflies and hoverflies from feeding on the flowers. However, experiments carried out in a wind tunnel showed that airborne pollen could potentially enter the netted flowers. When net bags were placed within vegetation, a moderate wind speed of 1.29 m/s caused air movement within bags of between 0.26 and 0.28 m/s. When the wind speed was increased, air movement inside net bags also rose, albeit at a slower rate. Therefore, wind pollination could not be entirely dismissed as a factor influencing the seed set in netted flowers. However, it was felt that in order not to restrict thrips movement, a smaller mesh size should not be used. Finally, Treatment 3 was a control in which the flowering shoots were not bagged but fully exposed to all insects and to the wind.

Forty replicates were spaced out on the heathland and the treatments were left *in situ* for two months until the time when seeds were ripe enough to be seen under the dissecting microscope. At that time, ovaries were dissected and the seeds counted per fruit.

6.3 RESULTS

6.31 Study 1: the abundance of thrips

Old and restored heathlands showed similar abundance of thrips in both *Calluna vulgaris* (Mann-Whitney U = 656, p = 0.22), *Erica cinerea* (Mann-Whitney U = 1491, p = 0.084) and *Erica tetralix* (Mann-Whitney U = 8695, p = 0.46) (Table 6.1).

On both types of heathland, the number of thrips in *E. cinerea* varied significantly over the season (old sites: Kruskal-Wallis H = 31.03, d.f. = 5, $p < 0.001$; restored sites: Kruskal-Wallis H = 20.63, d.f. = 5, p = 0.001). This was the case also for *E. tetralix* (old sites: Kruskal-Wallis H = 19.08, d.f. = 5, p = 0.002; restored sites: Kruskal-Wallis H = 26.01, d.f. = 5, $p < 0.001$), but not for *Calluna* (old sites: repeated measures ANOVA, $F_{(3, 39)} = 0.8$, p = 0.5; restored sites: repeated measures ANOVA, $F_{(3, 39)} = 1.40$, p = 0.26).

Figure 6.1 shows thrips abundance in the ericaceous plants on a heathland, Holton Lee Restored, from June until September. The graph was produced by multiplying the average number of thrips per flower, per sampling date, with the abundance of each of the three flower species at each date. Thrips in *Calluna* appeared to have two peaks in abundance, while thrips in *E. cinerea* peaked once in late July. The thrips in *E. tetralix* were more constant over the season.

6.32 Study 2: thrips pollination on a restored heathland

Figure 6.2 shows the seed set for each of *Calluna vulgaris*, *Erica cinerea* and *Erica tetralix*. In each species, thrips were responsible for a significant fraction of the total seed set. By subtracting the value for the bagged treatment (Treatment 1) from that of the netted treatment (Treatment 2), and relating this value to that of the control (Treatment 3) it is possible to calculate the percentage seed set caused by thrips. For *Calluna*, this value was between 46.09% and 55.19%, for *E. cinerea* it was between 29.01% and 45.26%, while for *E. tetralix* it was between 28.04% and 38.03%.

6.4 DISCUSSION

Thrips were abundant on all the heathlands and responsible for a significant fraction of the seeds produced. In this section I first review these findings and then I discuss the importance of thrips as pollinators. Before I conclude, I discuss the potential role of wind pollination in the present results.

6.41 Thrips on old and restored heathland

Thrips were common in all three ericaceous plant species on both the old and restored heathlands. Since these thrips feed inside their host flowers, they are very unlikely to exhibit different pollination behaviour on old and restored heaths. Therefore, thrips presence and abundance has been reinstated during the 10 years following restoration, and the results for Holton Lee Restored are concluded to be representative for these heathlands.

Both of the thrips species, which Hagerup (1950) and Hagerup and Hagerup (1953) recorded as pollinators of *Calluna vulgaris* and *Erica tetralix*, *Ceratothrips ericae* and *Frankliniella intonsa*, are both very common in England (Kirk 1996), and the former is, as the name indicates, particularly associated with ericoids. It is therefore likely that these were also the two most common species in the present study.

6.42 Seed set

Thrips accounted for large fractions of the seeds produced in the three ericaceous species. Because the fractions were so large, it illustrates how misleading community pollination studies can be if they only consider subsets of the community. An individual thrips is small and may not effect much pollination, but because of the sheer abundance of thrips, they are significant pollinators. For example, a total of 352 insects were caught visiting flowers on Holton Lee Restored during the quantitative sampling in 2001 (Chapter 3; Table 3.1). In contrast, the total abundance of thrips for two transects over the entire season would be estimated at more than 20,000 for that same heathland (Figure 6.1).

Did thrips actually use the netted flowers? Thrips mortality may be caused by many factors, including predation and pathogens. When dissecting old flowers, one occasionally comes across the dry remains of thrips. This also happened when old flowers were investigated for the seed content of their ovaries. From this I conclude that thrips had indeed used the netted flowers.

Thrips may also be significant pollinators of other heathland plants than just the three ericoids. For example, heath milkwort, *Polygala serpyllifolia* Hosé, which was recorded with low abundance at Hyde Old and Morden Old (Chapter 3; Figure 3.5 and Figure 3.6), was not observed to be visited by any insect during the quantitative sampling. Yet in an investigation of *P. serpyllifolia* flowers (not reported in this thesis), thrips were found in those flowers. Because the flowers were small and infrequent, it is possible that thrips could be the most important and possibly the sole visitors to *P. serpyllifolia*.

6.43 Much ado about selfing

From a plant point of view, thrips may not be ideal pollinators since they are likely to effect more self-pollination than cross-pollination (Hagerup and Hagerup 1953). Mahy and Jacquemart (1998; 1999) found that Belgian populations of *Calluna vulgaris* were highly self-sterile: when self-pollinated, the species produced 75% fewer seeds relative to cross-pollinated flowers. This is intriguing given that netted *Calluna* flowers produced about half the number of seeds relative to control flowers. Why is this difference not greater? If thrips activity and behaviour was comparable among netted flowers and controls, and if selfing was predominant in thrips pollination, it must be assumed that the additional seeds produced in the controls were likely to be both caused by larger insects and be a result of cross-pollination. However, if the figure of Mahy and Jacquemart (1998; 1999) is valid also for the Dorset heathlands, the pollination activity carried out by thrips appears to greatly outnumber that of other insects such that, although only about 25% of selfing events lead to seed set, the result for netted flowers is still about half the number of seeds produced relative to that in controls. In the controls, flowers selfed by thrips are more likely to produce seeds because they stand a higher chance of being cross-pollinated by other insects as well. Future work should investigate the proportion of seeds that result from thrips-mediated self-pollination with respect to the relative fitness of these seeds.

The seeds of ericaceous plants are small and numerous. They are relatively long lived and survive in the soil seed bank until conditions arise that facilitate germination (Bakker *et al.* 1996; Thomson and Band 1997). *Calluna vulgaris* is not known to germinate under its own canopy (Watt 1955) and it has seeds that can survive for over 100 years (Thomson and Band 1997). Although it is possible that the benefits of having more seeds in the soil might outweigh the costs of increased inbreeding, it is also possible that seeds resulting from self-pollination are less viable than those resulting from cross-pollination (e.g. Herlihy & Eckert

2002). On the Dorset heathlands, *Calluna*, *E. cinerea* and *E. tetralix* form extensive populations. Where heathland has long been established on a soil, cohorts of seedlings appear from the soil seed bank following disturbance, such as after a low-intensity fire. If selfed seeds are less viable than out-crossed seeds, the relative proportion of out-crossed seeds in the soil seed bank should increase over time. Therefore, selfing may not be a problem for the heathland species, provided that disturbance, and thus the dependence upon recruitment from the soil seed bank, happens at long enough intervals.

6.44 Wind pollination

The possibility remains that netted flowers experienced some wind pollination. It was noted earlier that studies have ascribed pollination in bagged *Calluna* flowers to the wind, although thrips could also have played a part. Here I risk drawing the equally erroneous conclusion of ascribing pollination to thrips, when the wind could be a factor also. However, wind speed translated poorly into air movement inside net bags. At moderate wind, the air movement inside net bags was only about 20% of the wind speed outside the bags. This proportion decreased as the wind increased. In contrast, the seed set in bags was between 30% and 50% of that of the controls. If the wind were responsible for the seed set in netted flowers, we would expect these proportions to be lower. Alternatively, the seed set should have been higher in the controls, unless these had reached maximum seed production, but this is unlikely, at least for *Calluna* (Pywell *et al.* 1996; Mahy *et al.* 1998).

The flower of *Calluna* is an open structure, which produces copious amounts of pollen and the species may be adapted to a combination of wind and insect pollination (Herrera 1987; Mahy *et al.* 1998). It is difficult to locate studies in the literature regarding wind pollination in *Erica cinerea* and *Erica tetralix*, and the flower morphology of these species does not seem to encourage wind pollination, although the genus *Erica* contains species that exhibit both wind and insect pollination (Herrera 1987). Hagerup and Hagerup (1953) noted that late in a flower's life, cross-pollination would be more likely in *E. tetralix*, because the stigma then protrudes out of the corolla and is exposed to the wind. However, neither in *E. cinerea* nor in *E. tetralix* do anthers protrude out of the corolla tube. Therefore, in comparison to *Calluna*, less pollen may enter air currents and this reduces the likelihood of wind pollination in these species. This should be tested in future studies. For example, a treatment could consider netted flowers, which were treated with a systemic insecticide at

regular intervals to prevent insect pollination, while allowing for wind pollination. Such an approach was not possible in the current study due to time and financial constraints.

6.45 Concluding remarks

Thrips presence and abundance was similar across old and restored heathland. Because they greatly outnumber all other flower-interacting insects, thrips are probably responsible for a significant fraction of the pollination on heathlands. At the same time, however, thrips are micro-insects, which do not visit many flowers and which may affect more self-pollination than cross-pollination. Individuals of large insects, such as bees and hoverflies that can now be regarded as rare in the pollinator community (in comparison to the thrips), may effect much more pollination and facilitate a higher degree of cross-pollination. Consequently, when assessing the quality of pollinator species, their abundance, size and activity levels are all important variables that must be taken into account.

TABLES

Table 6.1 The number of thrips found per flower in the flowering stems of *Calluna vulgaris* and *Erica cinerea* and the umbel of *Erica tetralix*, respectively, on the 8 Dorset heathlands.

	Calluna vulgaris		*Erica cinerea*		*Erica tetralix*	
	Mean + SE	Median	Mean + SE	Median	Mean + SE	Median
Arne Old	0.04 ± 0.01	0	0.05 ± 0.02	0	0.13 ± 0.03	0.16
Arne Restored	0.06 ± 0.03	0	0.09 ± 0.03	0	0.18 ± 0.08	0.17
Gore Old	0.15 ± 0.05	0	0.07 ± 0.03	0	0.26 ± 0.06	0.21
Holton Restored	0.08 ± 0.03	0	0.08 ± 0.03	0	0.14 ± 0.04	0.00
Hyde Old	0.22 ± 0.10	0	0.12 ± 0.03	0	0.09 ± 0.02	0.22
Hyde Restored	0.08 ± 0.03	0	0.12 ± 0.03	0	0.11 ± 0.02	0.05
Morden Old	0.11 ± 0.04	0	0.03 ± 0.02	0	0.19 ± 0.04	0.00
Morden Restored	0.02 ± 0.01	0	0.09 ± 0.03	0	0.32 ± 0.10	0.29

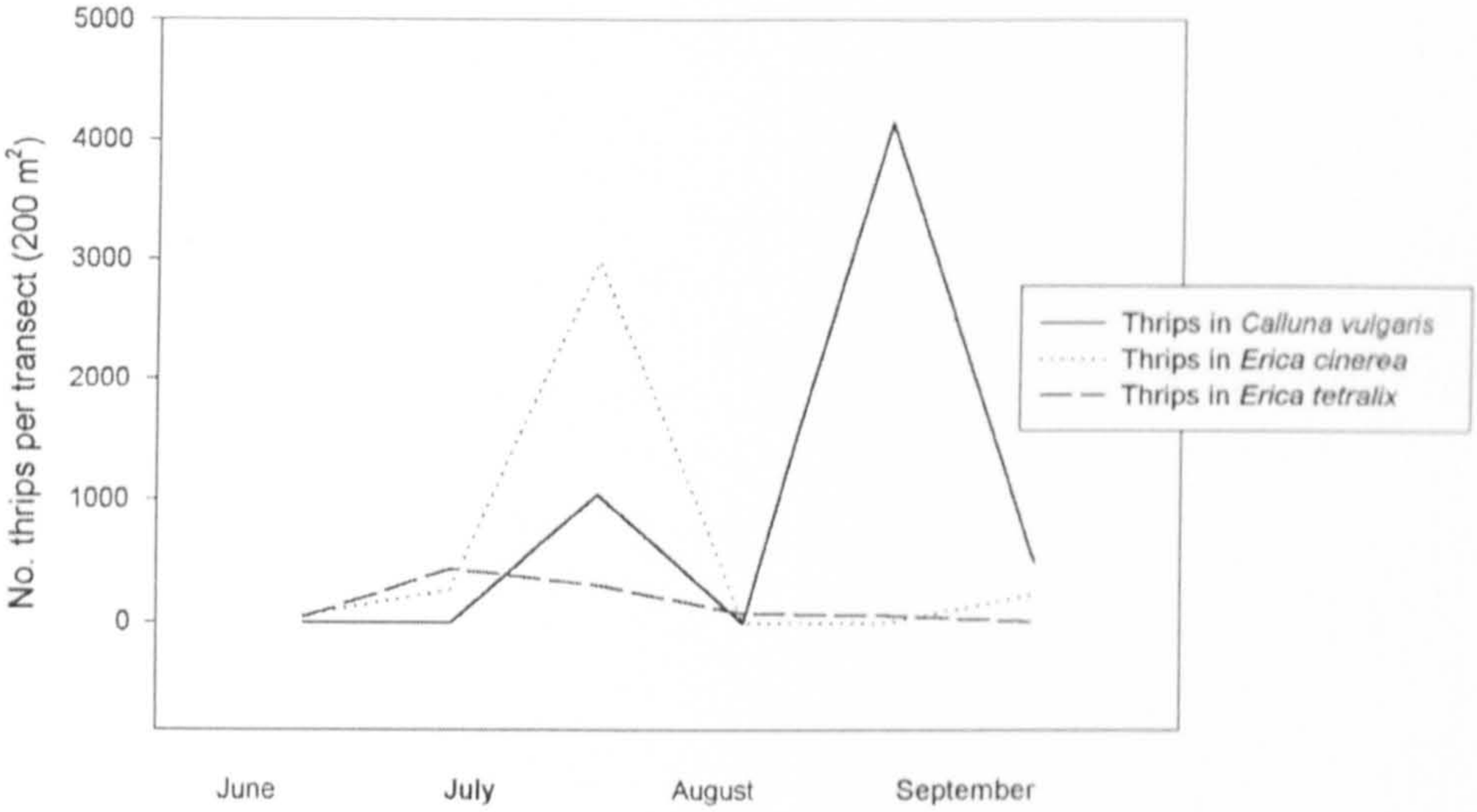

Figure 6.1 Estimate of thrips abundance on a heathland, Holton Lee Restored.

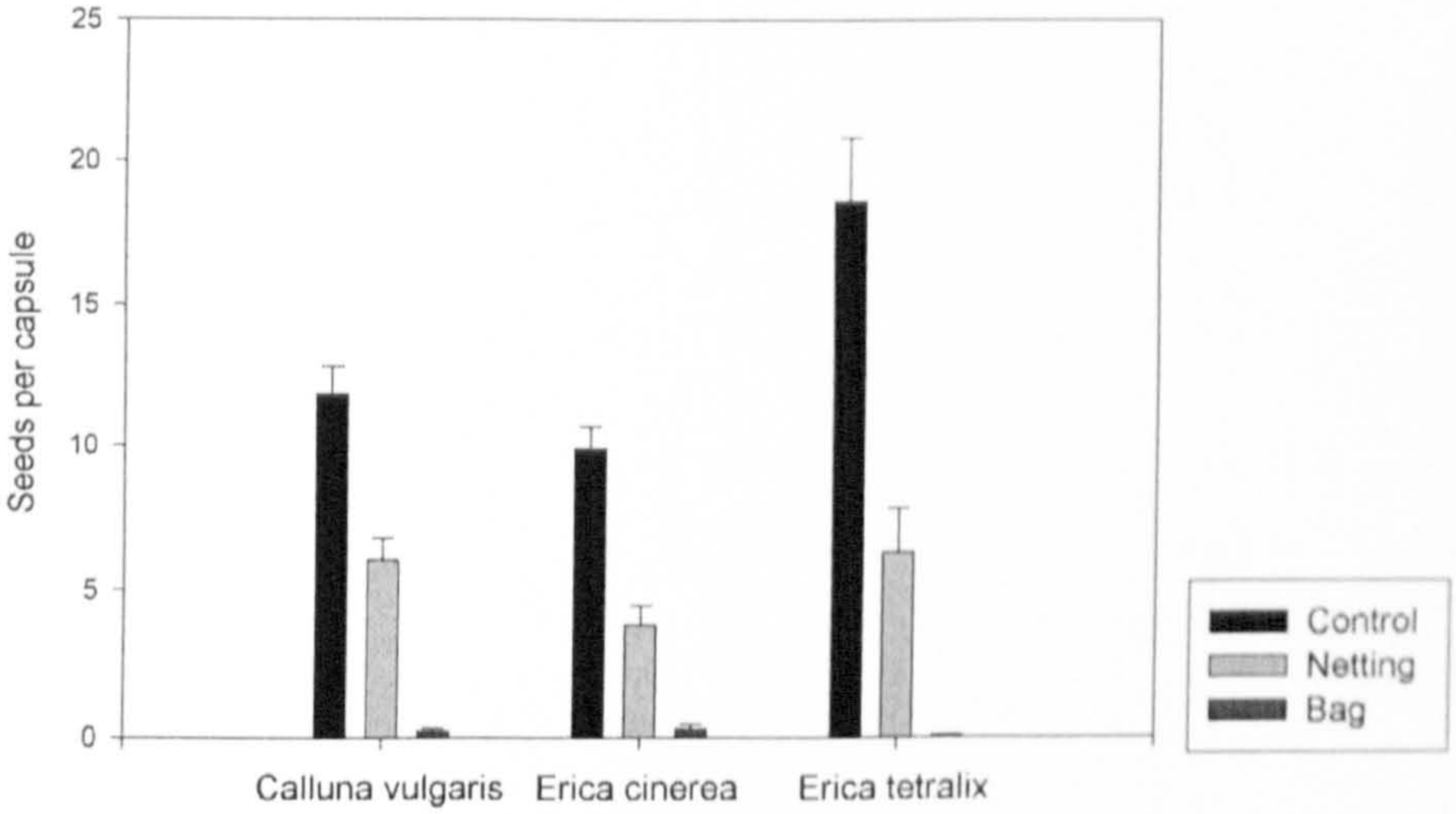

Figure 6.2 Mean number of seeds per capsule for the three ericaceous species in each of three treatments. Legend: Bag = Treatment 1: flowers were not exposed to any pollen vector, Netting = Treatment 2: flowers were exposed to thrips, Control = Treatment 3: flowers were exposed to all insects and to the wind.

CHAPTER SEVEN

Conclusion

CHAPTER SEVEN

Conclusion

7.1 The restoration of interactions vs. the restoration of species

Restoration ecology is similar to conservation biology insofar that emphasis is often placed on species rather than on processes. Counting species is both a convenient way of assessing the biodiversity value of a given study site and information to which the general public can easily relate. However, there are shortcomings with species counts as measures of structural biodiversity, because these measures do not tell us what the species do in their communities, nor how often. This problem is particularly stark when we consider mutualisms. For example, restoration projects are often evaluated in terms of plant species richness, with little or no regard to the insect pollinators of these plants. In an extreme example, plant species living in the absence of suitable pollinators could slowly be disappearing because no recruitment took place to compensate for losses due to age and chance events. Here a simple plant species count would fail to reveal the grave situation of those plants. Therefore, restoration projects must be evaluated with regards to their sustainability.

I consider the interactions between species and the relative abundance of those interactions as better units of measurement than the presence or absence of individual species for assessing the outcome of ecological restorations. Here I have focused on species interactions, although the data also provides information about structural biodiversity. I have obtained quantitative information of pollinators' foraging choices and their value as pollen carriers to the host plants. This has meant an improved ability to assess whether restoration schemes have reinstated an ecosystem process, namely pollination. Although the work was labour intensive, it was not as daunting a procedure as was once predicted (Waser *et al.* 1996). It took one worker one summer to collect the quantitative heathland interaction data and about one year to process and analyse the data. However, it should be stressed that lowland heathlands are relatively simple systems to work on and that no nocturnal work was carried out.

7.2 The failure in current restoration to consider replication

Since the nature of ecological restoration in practise is to achieve a satisfactory outcome with the limited funds available, restoration projects are rarely designed with regards to the rigorous statistical analysis that can only come from replication. This is a pity for two reasons: first, restoration experiments often fail to live up to the strict demands of scientific journals, wherefore experience, if published at all, is largely communicated through the journals of the restoration community, where it may not be read by more general ecologists. This lack of exposure to the wider scientific community slows down the evolution of the restoration ecology paradigm. Second, restoration experiments can provide ideal situations for testing ecological theories. Assembly rules are obvious examples, because they add complexity to the 'field of dreams' hypothesis (Luh and Pimm 1993; Palmer 1997): communities are not simply assemblages of all the species which have managed to reach the restored plot. The sequence in which these species arrived may affect the final structure of the community.

In the heathland study I used a paired experimental design. This allowed a quantification of the considerable variation among localities while at the same time it compared restored sites to nearby representatives of their own target state. However, the results cast further doubt on the usefulness of target sites in comparing structural biodiversity. Old heaths and meadows showed considerable variation and if a single site had been chosen as a target site, restoration might never have been achieved if defined in terms of the structure of the restored communities. Ideally a higher number of replicate sites would have been sampled, as this would have allowed for a more rigorous analysis that could have detected more subtle differences among the sites. However, it was not possible to locate more restored heaths of a similar age and management history in the Poole Basin. Nor would it have been feasible for one worker to process and analyse the data of many more sites. Moreover, the paired design was sufficient to compare and contrast patterns among old and restored heathlands. In retrospect, probably too few hay meadows were used and they were too diverse for this design to be successful.

7.3 What has been learned about plant-pollinator interactions?

Similar to Dicks (2002), the first conclusion is that the evidence confirms that plant-pollinator systems are highly generalized rather than specialized (Waser *et al.* 1996; Johnson and Steiner 2000). Both plants and insects make use of several partners, and this is

thought to reduce the risk of reproductive failure (Bond 1994). However, generalization was more common for plants than for insects, in part because there were many more insect species than plant species, and because the different flowering phenology in the plant community meant that only few species were in bloom at the same time.

Secondly, there is considerable spatial variation among insect communities. This means that such notions as the 'heathland pollinator community' implies a stability and constancy that is not supported by the data. Indeed, where species occurred that specialise on heathlands, these were rarely abundant. In contrast, opportunistic species that can be found in several habitats throughout the landscape were both widespread and abundant. Therefore, on the Dorset heathlands, the landscape is an important determinant of the kind of pollinators that are found there.

Thirdly, pollination biologists risk drawing misleading conclusions when focusing on subsets of the communities they study. For example, by leaving out thrips in the work on the heathlands, a very high number of flower-insect interactions would have been ignored. Since thrips may be responsible for up to half of the seeds produced in *Calluna vulgaris*, *Erica cinerea* and *Erica tetralix*, considerable error could be associated with studies on heathland pollination that only consider macro-insects. However, the failure to sample nocturnal flower visitors meant that even the present dataset is not entirely complete, despite sampling the 8 heathlands 8 times and recording interactions between at least 112 species of insect and 15 species of plant!

Fourthly, quantitative visitation webs and quantitative pollen transport webs are only the first steps towards true pollination webs (Memmott 1999). The next step must involve measures of the pollination potential for each species of insect, the number of flowers an individual can visit, etc. So far, such measures have only been worked out for individual plant species, rather than whole communities. However, researchers are beginning to investigate this aspect (Dicks 2002) and it is the obvious next step for heathland pollination research. Care must be taken to replicate such studies because of the huge spatial variability in pollinator communities. Such work must also ensure that the whole pollinator community is considered. Meanwhile, both the quantitative visitation and pollen transport webs are useful tools in their own right. The former show where insects prefer to feed and are therefore relevant for understanding the resource base for the insect community, something that is rarely worked out for whole communities. Quantitative pollen transport webs are useful, because they show which of the insect visitors are also pollen carriers,

although it must be stressed again that this does not necessarily mean that they carry out pollination services in proportion to their pollen loads.

Although the work shed light on the patterns of flower visitation and pollen transport, it did not consider what could be the best measure of restoration success in pollination systems; namely seed set. One reason for this was that although a diverse community of pollinators may actually be present on a restored heathland, there would be differences in pollination and seed set between this and old heathlands that related to the relative abundance of the plant species, since this influences where pollinators forage. Therefore, the best approach would not be to simply collect seed capsules and count the seed content. Furthermore, seed set could be a crude measure of restoration success, unless it incorporated some measure of seed viability. Besides, the seed set does not reveal who the pollinator was. In a series of studies, the pollination effected by the individual species in a pollination system could be quantified, similar to the work presented here on the seed set effected by thrips on heathlands. Yet another approach would be to carry out bioassays on old and restored heathlands. For example, a set number of flowering, potted plants could be placed in the field for a set time and then be removed for seed development in the absence of further pollination. While such a study was beyond the scope of this work, a similar approach was attempted in the field season of 2002, where all but a set number of Dwarf Gorse (*Ulex minor*) flowers were shaved off branches to create standardized flower units on old and restored heathlands. However, the work is not reported in this thesis, because the majority of the initial flowers were aborted, seed development in the remainder was too slow to be processed and analysed here and because numerous new flowers developed over the 2-month period. In fact, *U. minor* has a long flowering season, perhaps because visits to this species are rare when both *U. minor* and the ericoids flower.

7.4 Has investigating interactions provided a better assessment of restoration success?

Although ecological restorations are carried out for a range of reasons, an assessment of their success should consider the sustainability of the restored communities. For example, the restored meadow Brandon Hill was established merely as a wildflower meadow. Since it was very rich in plant species, it might be assumed that the restoration has been successful. However, unless quantitative sampling was carried out to investigate the plant-pollinator interactions, it would not have been known if the plant species were visited and if

their pollen was being carried by pollinators. A census could be repeated over time to investigate if populations were increasing, decreasing or stable.

On the heathlands, structural biodiversity varied among old and restored plots. Moreover, although heathland restoration reinstated a pollinator community with comparable visitation patterns to that of old heaths, the movement of pollen was not similar after ten years. However, this is argued to be related to age: as the heathlands mature, the plant species develop a proportional balance similar to that of old heathlands, and with this restoration of flower availability over the season, patterns are likely to be restored also.

7.5 Implications of this work for ecological restorations

In order to investigate the sustainability of a restored system, we need to understand what species do in ecosystems and whether there is redundancy built into the systems. For example, do certain species form compartments, which have to be reinstated if pollination is to occur at all? Do rare species exert an influence in or out of proportion to their abundance? With so many unknowns, it is imperative that restorationists seek to understand the ecology of the species they are dealing with, before attempting to restore the working relationships among species.

The implications of the present work for ecological restorations are fourfold: 1) the objectives for carrying out restoration must be clearly defined in order to assess whether or not these objectives have been met. Restoration ecology is a science that grows in response to our increasing needs to repair ecological damage, but it need not be a tool merely for land managers. Carefully planned and executed restoration projects can greatly expand and test our ecological knowledge; 2) investigating the structural biodiversity of restored plots is useful information only when we understand what role the species perform in their community and who they interact with; 3) restorationists need to work in concert with succession and within the context of landscape. Adhering too strictly to a vision of what ought to be, rather than what can be, is almost certain to result in failure; and 4) because systems are generalised, plants may not be pollinator limited, although the frequency with which the various pollinator species interact with the plants needs to be quantified. However, it should be investigated if suitable pollinators are available for all plants in a community, particularly if compartments could be regular features of the systems.

7.6 Future directions

The study has highlighted three main areas in need of more research: 1) efforts should now be made to construct true pollination webs, partly because only then can we quantify the true level of redundancy in the pollination systems. These studies should include the relative seed set caused by the various pollinator species, because seed set is the ultimate measure of reproductive success. This work should incorporate measures of inbreeding and seed viability; 2) the method for detecting small compartments in plant-pollinator webs should be improved. Although compartments may not be a regular feature of the heathlands, small compartments were unlikely to be detected and, in some cases, impossible to detect with the methods of Rafaelli and Hall (1992); and 3) the effect of *Apis mellifera* on competing bees should be investigated further, particularly with reference to whether a more sensitive management of this species would be beneficial to bee conservation, and especially those species, which are currently declining.

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APPENDICES

APPENDIX C2: plant and insect species in four English hay meadows

Legend:
- Species recorded in transects

Plant species	Family	Authority	Flower group	Meadow 1	Meadow 2	Meadow 3	Meadow 4
Bellis perennis	Asteraceae	L.	3b	•	•	•	•
Cardamine pratensis	Brassicaceae	L.	3a		•		
Carduus acanthoides	Asteraceae	L.	3b			•	
Carum carvi	Apiaceae	L.	2b				•
Centaurea nigra	Asteraceae	L.	3b	•	•	•	•
Centaurium erythraea	Gentianaceae	Rafn	5a	•			
Cerastium fontanum	Caryophyllaceae	Baumg.	3a	•	•	•	•
Conopodium majus	Apiaceae	(Gouan) Loret	2b		•	•	
Crepis biennis	Asteraceae	L.	3b	•			
Crepis capillaris	Asteraceae	(L.) Wallr.	3b	•		•	•
Crepis vesicaria	Asteraceae	L.	3b	•			
Dactylorhiza fuchsii	Orchidaceae	(Druce) Soó	4a	•		•	
Daucus carota	Apiaceae	L.	2b	•		•	
Galium verum	Rubiaceae	L.	2b			•	
Geranium columbinum	Geraniaceae	L.	3a	•	•		•
Geranium pratense	Geraniaceae	L.	3a				•
Heracleum sphondylium	Apiaceae	L.	2b		•	•	•
Hypochaeris radicata	Asteraceae	L.	3b	•		•	•
Knautia arvensis	Dipsacaceae	(L.) Coult.	2b	•			•
Leontodon hispidus	Asteraceae	L.	3b			•	•
Leucanthemum vulgare	Asteraceae	Lam.	3b	•	•	•	•
Lotus corniculatus	Fabaceae	L.	4a	•	•	•	•
Lotus pedunculatus	Fabaceae	Cav.	4a				•
Medicago lupulina	Fabaceae	L.	4b	•		•	•
Orchis morio	Orchidaceae	L.	4a	•		•	
Orobanche minor	Orobanchaceae	Sm.	4a	•			
Pilosella officinarum	Asteraceae	Schultz & Sch. Bip.	3b			•	•
Plantago lanceolata	Plantaginaceae	L.	1b		•		•
Polygala vulgaris	Polygalaceae	L.	2a			•	
Potentilla erecta	Rosaceae	(L.) Raeusch.	2a			•	
Prunella vulgaris	Lamiaceae	L.	4a	•	•	•	
Ranunculus acris	Ranunculaceae	L.	2a	•	•	•	•
Ranunculus bulbosus	Ranunculaceae	L.	2a			•	•
Ranunculus repens	Ranunculaceae	L.	2a	•	•	•	•
Rhinanthus minor	Scrophulariaceae	L.	4a	•		•	
Senecio jacobaea	Asteraceae	L.	3b	•		•	•
Stachys officinalis	Lamiaceae	(L.) Trevis	4a				•
Taraxacum Agg.	Asteraceae	Wigg.	3b	•		•	
Trifolium pratense	Fabaceae	L.	4b	•	•	•	•
Trifolium repens	Fabaceae	L.	4b	•		•	•
Vicia cracca	Fabaceae	L.	4a		•		•
Vicia sativa	Fabaceae	L.	4a	•	•		•

Insect species	Order	Authority	Meadow 1	Meadow 2	Meadow 3	Meadow 4
Andrena bicolor	Hymenoptera	Fabr.				•
Andrena cineraria	Hymenoptera	L.				•
Andrena flavipes	Hymenoptera	Panzer				•
Andrena haemorrhoa	Hymenoptera	Fabr.		•		•
Andrena nigroaenea	Hymenoptera	Kirby		•		
Andrena pubescens	Hymenoptera	Olivier	•			•
Andrena saundersella	Hymenoptera	Perkins			•	
Anthomyiidae spp	Diptera		•	•	•	•
Apis mellifera	Hymenoptera	L.	•		•	•
Bellardia pandia	Diptera	Walker	•			•
Bombus hortorum	Hymenoptera	L.				•
Bombus muscorum	Hymenoptera	L.	•			•
Bombus pascuorum	Hymenoptera	Scop.	•	•	•	•
Bombus pratorum	Hymenoptera	L.	•			
Bombus ruderarius	Hymenoptera	Müller	•	•	•	•
Bombus ruderatus	Hymenoptera	Fabr.	•	•		•
Bombus terrestris/lucorum	Hymenoptera	L.	•	•	•	•
Byturus sp.	Coleoptera			•		
Calliphora vomitoria	Diptera	L.				•
Cetonia aurata	Coleoptera	L.				•
Cheilosia albitarsis	Diptera	Meigen		•		•
Cheilosia bergenstammi	Diptera	Becker				•
Cheilosia intonsa	Diptera	Loew	•	•	•	•
Chrysotoxum bicinctum	Diptera	L.	•			•
Coccinellidae sp.	Coleoptera					•
Coenosia tigrina	Diptera	Fabr.		•	•	
Colletes fodiens	Hymenoptera	Geoff.				•
Dolichopus trivialis	Diptera	Haliday.			•	
Empis livida	Diptera	L.		•		
Episyrphus balteatus	Diptera	Deg.	•	•		•
Eristalis arbustorum	Diptera	L.	•			•
Eristalis tenax	Diptera	L.	•		•	•
Euclidia glyphica	Lepidoptera	L.		•		
Fannia umbratica	Diptera	Collin & Veralli Stein	•			•
Helicophagella crassimargo	Diptera	Pandellé			•	•
Helicophagella sp.	Diptera				•	
Helophilus pendulus	Diptera	L.	•			
Hemiptera 1	Hemiptera					•
Hemiptera 2	Hemiptera				•	
Lasioglossum albipes	Hymenoptera	Fabr.	•			
Lasioglossum calceatum	Hymenoptera	Scop.	•		•	•
Lasioglossum fulvicorne	Hymenoptera	Kirby	•			
Lasioglossum leucozonium	Hymenoptera	Schrank	•			•
Lasioglossum smeathmanellum	Hymenoptera	Kirby	•			•
Lasioglossum villosulum	Hymenoptera	Kirby				•
Lasius niger Agg.	Hymenoptera	L.				•
Lejogaster metallina	Diptera	Fabr.			•	•
Lindenius albilabris	Hymenoptera	Fabr.	•			

Insect species	Order	Authority	Meadow 1	Meadow 2	Meadow 3	Meadow 4
Lonchoptera lutea	Diptera	Panzer			•	
Lucilia sericata	Diptera	Meigen				•
Maniola jurtina hispulla	Lepidoptera	Esper	•		•	
Megachile centuncularis	Hymenoptera	L.		•		•
Melanargia galathea galathea	Lepidoptera	L.	•			
Meligethes spp	Coleoptera		•		•	
Merodon equestris	Diptera	Fabr.		•		
Metasyrphus luniger	Diptera	Meigen		•	•	
Oedemera lurida	Coleoptera	Marseul			•	•
Oedemera nobilis	Coleoptera	Scop.	•		•	•
Parasitica 1	Hymenoptera					
Parasitica 2	Hymenoptera					•
Parasitica 3	Hymenoptera		•			•
Piezodorus lituratus	Coleoptera	Fabr.				•
Platycheirus albimanus	Diptera	Fabr.				•
Platycheirus angustatus	Diptera	Zett.				•
Pollenia pediculata	Diptera	Macquart		•		
Pollenia rudis	Diptera	Fabr.			•	
Pyronia tithonus	Lepidoptera	L.	•			
Rhagio tringarius	Diptera	L.			•	
Rhagonycha lutea	Coleoptera	Müller				•
Rhinophora lepida	Diptera	Meigen				•
Sarcophaga carnaria	Diptera	L.	•	•		•
Sarcophaga lasiostyla	Diptera	Macquart		•		•
Sarcophaga sp.	Diptera		•	•		
Sarcophaga variegata	Diptera	Scop.		•		•
Scathophaga stercoraria	Diptera	L.	•	•	•	•
Siphona cristata	Diptera	Fabr.	•			
Sphaerophoria menthastri	Diptera	L., *sensu* Vockeroth			•	
Sphaerophoria scripta	Diptera	L.	•	•	•	•
Syrphus ribesii	Diptera	L.				•
Thymelicus flavus	Lepidoptera	Brunnich			•	
Unidentified Diptera sp.	Diptera		•			
Volucella bombylans	Diptera	L.		•		
Xylota florum	Diptera	Fabr.				•
Zygaena filipendulae stephensi	Lepidoptera	Stainton	•		•	
Zygaena trifolii decreta	Lepidoptera	Verity	•			•

APPENDIX C3: plant and insect species on eight English lowland heathlands

Legend:

- • Species recorded in transects
- o Plant species observed on a site but not recorded in transects
- P Plant species not observed on the site but recorded with a minimum of 5 grains in the pollen load of at least one insect specimen

Plant species	Family	Authority	Arne Old	Arne Restored	Gore Old	Holton Restored	Hyde Old	Hyde Restored	Morden Old	Morden Restored
Bellis perennis	Asteraceae	L.				o				
Calluna vulgaris	Ericaceae	(L.) Hull	•	•	•	•	•	•	•	•
Centaurium erythraea	Gentianaceae	Rafn					P	o		
Cerastium fontanum	Caryophyllaceae	Baumg.	o	•		•	o			
Chamerion angustifolium	Onagraceae	Holub			•					
Cirsium palustre	Asteracea	(L.) Scop.					P	•	P	P
Erica cinerea	Ericaceae	L.	•	•	•	•	•	•	•	•
Erica tetralix	Ericaceae	L.	•	•	•	•	•	•	•	•
Digitalis purpurea	Scrophulariaceae	L.				o	o	o		
Galium saxatile	Rubiaceae	L.						o		
Hypochaeris glabra	Asteraceae	L.	o	o	P	o	P	•	o	o
Hypochaeris radicata	Asteraceae	L.				o	o	o		
Leontodon hispidus	Asteraceae	L.						o		
Leontodon saxatilis	Asteraceae	Lam.			P		P	o		
Lotus corniculatus	Fabaceae	L.						o		
Polygala serpyllifolia	Polygalaceae	Hosé			o		•		•	
Potentilla erecta	Rosaceae	L.				o				
Prunella vulgaris	Lamiaceae	L.						•		
Pulicaria dysenterica	Asteraceae	(L.) Bernh.						o		
Ranunculus acris	Ranunculaceae	L.						o		
Ranunculus repens	Ranunculaceae	L.								o
Rhododendron ponticum	Ericaceae	L.	o	•		P	•	o	o	o
Rumex acetosella	Polygonaceae	L.		•		•		•	o	•
Senecio jacobaea	Asteraceae	L.	o				P	•	P	•
Taraxacum Agg.	Asteraceae	Wigg.		o				o		
Teucrium scorodonia	Lamiaceae	L.							o	
Ulex europaeus	Fabaceae	L.	•	•	•	•	o	•	•	P
Ulex gallii	Fabaceae	Planch.			•	•	o	o		
Ulex minor	Fabaceae	Roth	•	•	•	•	•	•	•	•
Veronica chamaedrys	Scrophulariaceae	L.					o			

Insect species	Order	Authority	Arne Old	Arne Restored	Gore Old	Holton Restored	Hyde Old	Hyde Restored	Morden Old	Morden Restored
Aedes caspius	Diptera	Pallas		•						
Aglais urticae	Lepidoptera	L.			•		•			•
Andrena dorsata	Hymenoptera	Kirby	•				•	•		
Andrena fuscipes	Hymenoptera	Kirby	•	•	•	•	•	•		
Andrena ovatula	Hymenoptera	Kirby	•		•		•		•	
Apion ulicis	Coleoptera	Forster	•	•	•	•			•	
Apis mellifera	Hymenoptera	L.	•	•	•	•	•	•	•	•
Aricia agestis	Lepidoptera	Denis & Schiffermüller							•	
Atylotus latistriatus	Diptera	Brauer	•							
Bellardia pandia	Diptera	Walker					•	•		
Bellardia viarum	Diptera	Rob. Des.				•				
Bibio nigriventris	Diptera	Haliday		•				•		
Bicellaria pilosa	Diptera	Lundbeck						•		
Bombus hortorum	Hymenoptera	L.							•	
Bombus humilis	Hymenoptera	Illiger	•	•	•	•	•	•	•	
Bombus jonellus	Hymenoptera	Kirby	•	•	•	•	•	•	•	•
Bombus lapidarius	Hymenoptera	L.			•	•	•	•	•	•
Bombus lucorum/terrestris	Hymenoptera	L.	•	•	•	•	•	•	•	•
Bombus muscorum	Hymenoptera	L.	•			•		•		
Bombus pascuorum	Hymenoptera	Scop.	•		•	•	•	•	•	•
Brachicoma devia	Diptera	Fall.					•	•		
Calliphora vicina	Diptera	Rob. Des.		•						•
Ceratopogonidae indet.	Diptera		•							
Cerceris arenaria	Hymenoptera	L.						•		•
Ceridomyiidae indet.	Diptera									•
Chalcidoidea indet.	Hymenoptera		•							
Chironomus annularius	Diptera	Deg.								•
Coccinella 7-punctata	Coleoptera	L.				•		•		
Coenosia indet.	Diptera						•			
Coenosia tigrina	Diptera	Fabr.			•		•			
Coleoptera indet. 1	Coleoptera				•					
Coleoptera indet. 2	Coleoptera					•				
Coleoptera indet. 3	Coleoptera					•				
Coleoptera indet. 4	Coleoptera					•				
Colletes succinctus	Hymenoptera	L.	•	•	•		•	•	•	•
Cynthia cardui	Lepidoptera	L.					•			
Delia platura	Diptera	Meigen	•		•					
Empis praevia	Diptera	Collin					•			
Enallagma cyathigerum	Odonata	Charpentier								•
Epistrophe grossulariae	Diptera	Meigen		•	•	•	•	•		•
Episyrphus balteatus	Diptera	Deg.	•	•	•	•	•	•	•	•
Eristalis abusivus	Diptera	Collin								•
Eristalis arbustorum	Diptera	L.						•	•	
Eristalis pertinax	Diptera	Scop.		•						
Eristalis tenax	Diptera	L.	•		•	•	•		•	•
Eudasyphora cyanella	Diptera	Meigen					•			

Insect species	Order	Authority	Arne Old	Arne Restored	Gore Old	Holton Restored	Hyde Old	Hyde Restored	Morden Old	Morden Restored
Eumerus strigatus	Diptera	Fall.			•		•			
Formica fusca	Hymenoptera	L.				•	•	•	•	•
Formica rufa	Hymenoptera	L.	•	•		•				
Graphomyza picta	Diptera	Zett.				•				
Hebecnema umbratica	Diptera	Meigen					•			
Helina reversio	Diptera	Harris				•				
Helophilus pendulus	Diptera	L.		•	•	•	•	•	•	•
Hydrellia griseola	Diptera	Fall.					•			
Hydrophoria lancifer	Diptera	Harris				•				
Hydrotaea irritans	Diptera	Fall.					•			
Inachis io	Lepidoptera	L.			•					
Ischnorhynchus geminatus	Hemiptera	Fieb.				•			•	
Lasioglossum indet.	Hymenoptera		•							
Lasioglossum lativentre	Hymenoptera	Schenk					•			
Lasioglossum prasinum	Hymenoptera	Smith	•		•				•	
Lasius niger Agg.	Hymenoptera	L.					•			
Linnaemyia vulpina	Diptera	Fall.			•	•	•	•	•	•
Lucilia caesar	Diptera	L.							•	
Lucilia richardsi	Diptera	Collin			•					
Lucilia sericata	Diptera	Meigen			•					
Machimus atricapillus	Diptera	Fall.								•
Melanargia galathea	Lepidoptera	L.						•		
Melinda gentilis	Diptera	Rob. Des.					•			
Metasyrphus corollae	Diptera	Fabr.	•	•	•	•	•	•	•	•
Metasyrphus latifasciatus	Diptera	Macquart			•					
Metasyrphus luniger	Diptera	Meigen	•		•	•	•	•		
Musca autumnalis	Diptera	Deg.		•			•		•	
Myathropa florae	Diptera	L.								•
Myopa fasciata	Diptera	Meigen			•					
Neomyia cornicina	Diptera	Fabr.	•			•				
Neomyia viridescens	Diptera	Rob. Des.	•							
Odontothrips ulicis	Thysanoptera	Haliday	•							
Orthocladiinae indet.	Diptera							•		
Parasitica indet.	Hymenoptera		•		•		•	•	•	
Philanthus triangulum	Hymenoptera	Fabr.		•	•				•	
Phora indet.	Diptera		•							
Platycheirus albimanus	Diptera	Fabr.			•	•	•	•	•	
Platycheirus scutatus	Diptera	Meigen	•							•
Pollenia amentaria	Diptera	Scop.			•			•		
Pollenia angustigena	Diptera	Wainwright					•	•		
Pollenia rudis	Diptera	Fabr.			•	•				
Pollenia viatica	Diptera	Rob. Des.				•	•	•		
Polydrusus confluens	Coleoptera	Stephens				•		•		
Psithyrus vestalis	Hymenoptera	Geoff.							•	
Rhagio tringaria	Diptera	L.					•			
Rhagonycha fulva	Coleoptera	Scop.		•	•	•	•	•	•	

Insect species	Order	Authority	Arne Old	Arne Restored	Gore Old	Holton Restored	Hyde Old	Hyde Restored	Morden Old	Morden Restored
Rhingia campestris	Diptera	Meigen			•					
Sarcophaga carnaria	Diptera	L.			•		•	•		
Sarcophaga incisilobata	Diptera	Pandellé			•					
Sarcophaga indet.	Diptera		•		•	•	•	•	•	•
Sarcophaga subvicina	Diptera	Rohdendorf					•			
Sarcophaga variegata	Diptera	Scop.			•			•		
Scathophaga stercoraria	Diptera	L.	•	•				•		
Sepsidae indet.	Diptera						•			•
Sericomyia silentis	Diptera	Harris		•		•		•		•
Sericus brunneus	Coleoptera	L.					•			
Sicus ferrugineus	Diptera	L.	•		•				•	•
Siphona urbana	Diptera	Harris							•	
Sphaerophoria menthastri	Diptera	L., *sensu* Vockeroth				•				
Sphaerophoria philanthus	Diptera	Meigen				•	•			
Sphaerophoria scripta	Diptera	L.	•	•	•		•	•	•	•
Syritta pipiens	Diptera	L.		•	•		•			
Tachina grossa	Diptera	L.						•	•	
Tortricidae indet.	Lepidoptera		•							
Trypetoptera punctulata	Diptera	Scop.						•		
Vespula rufa	Hymenoptera	L.	•		•	•				

APPENDIX C5: honeybee and bumblebee on nineteen old lowland heathlands in England

The abundance of bees sampled along transects on 19 old heathlands. Brackets list the flower species, which individual bees visited. Codes: Cv = *Calluna vulgaris*, Ec = *Erica cinerea*, Et = *Erica tetralix*, Ug = *Ulex gallii* and Um = *Ulex minor*.

Site	Grid Reference	*Apis mellifera*	*Bombus humilis*	*Bombus jonellus*	*Bombus lapidarius*	*Bombus lucorum/terrestris*	*Bombus pascuorum*
Winfrith Heath	SY8086	38 (Ec)			1 (Ec)	3 (Ec)	
Coombe Heath	SY8785	4 (Cv,Ec)		2 (Ec)	5 (Ec)	2 (Ec)	
Higher Hyde	SY8590	10 (Ec,Et)		1 (Ec)		4 (Ec)	
Studland Heath	SZ0284	73 (Cv,Ec,Et)				2 (Ec)	
Hartland Moor	SY9485	21 (Cv,Ec)				4 (Ec)	
Morden Bog	SY9192	23 (Ec,Et)			4 (Ec)	10 (Ec)	2 (Ec)
Arne	SY9788	81 (Ec,Et)				2 (Ec)	1 (Ec)
Stokeford Heath	SY8788	4 (Ec)		3 (Ec)	2 (Ec)	12 (Ec)	
Upton Heath	SY9895	41 (Ec)			1 (Cv)	5 (Cv)	
Cranborne Common	SU1011	62 (Ec, Et)		2 (Ec)		3 (Ec)	
Stephen's Castle	SU0909	41 (Ec)		2 (Ec)	3 (Ec)	5 (Ec)	
Lower Hyde	SY8891	6 (Ec,Et)			1 (Ec)	14 (Ec)	
Great Ovens	SY9390	23 (Cv,Ec)	1 (Ug)	2 (Ec,Et)		2 (Ec)	
Canford Heath	SZ0396	12 (Cv,Ec)		1 (Cv)	3 (Cv,Ec,Ug)	5 (Cv,Ec,Ug)	
Avon Heath North	SU1304	7 (Cv,Ec)				9 (Cv,Ec)	3 (Um)
Avon Heath South	SU1302	7 (Cv,Ec)		2 (Cv)		4 (Cv,Ec)	1 (Ec)
Holt Heath	SU0604	77 (Cv,Ec)		1 (Ec)	2 (Ec,Um)	4 (Ec,Um)	
Sopley Common	SZ1398	30 (Cv,Ec)			1 (Ec)	3 (Ec)	
Town Common	SZ1496	27 (Cv,Ec)		1 (Ec)	7 (Ec)	7 (Ec)	2 (Um)
Total		587	1	17	30	100	9